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PART I.

1. THE CAUSES OF FLUCTUATIONS IN TURGESCENCE IN THE MOTOR ORGANS OF LEAVES.

2. A NEW AND PARASITIC SPECIES OF CHOAN PHORA.

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THE

CAUSES OF FLUCTUATIONS IN TURGESCENCE

IN THE

MOTOR ORGANS OF LEAVES

INTRODUCTION

THE following pages contain an attempt to demonstrate that the great majority, if not all, of the transient spontaneous movements of higher vegetable organisms, whether of a nyctitropic character or arising in connection with other conditions than the incidence or removal of sunlight, are not dependent on the presence of any specially irritable and contractile protoplasts within the motor organs, but on purely physical processes connected either with fluctuations in the osmotic capacities of the tissue elements, or with alterations in the relations existing between local or general supply and loss of water This may at first sight appear to be a retrograde view, but at the same time, I feel assured that it is more in accord both with actual fact and with evolutionary doctrine than that which is commonly accepted in Europe, at the present time, and it is one which I have arrived at only after more than ten years of almost continuous study of the subject

Conspicuous examples of transient spontaneous movements are relatively rare in plants in Europe and have therefore, to a great extent, been studied there in connection with tropical plants growing under very abnormal conditions This has not unnaturally given rise, on the one hand, to an over estimate of their exceptional character, and, on the other, to imperfect and erroneous conceptions in regard to the conditions under which they normally manifest themselves But within the tropics such movements and specially those of a nyctitropic character, are so widely diffused that they may readily be made the subject of continuous observation under normal conditions, and with this the tendency to ascribe them to exceptional causes is proportionately diminished

Observers in Europe unquestionably have many great advantages the climate is favourable to strenuous work, they possess very great advantages in regard to the ready acquisition of special apparatus, and they can constantly avail themselves of skilled criticism of any conclusions at which they may arrive But, at the same

time, they labour under certain disadvantages in the study of the physiology of tropical organisms. They cannot place the latter under strictly normal conditions, and are therefore constantly liable to assume that phenomena which present themselves under unnatural conditions may be taken to represent those occurring under natural ones. The phenomena of movement occurring in plants with their roots cramped within pots and exposed to quite abnormal atmospheric conditions can, in no sense, be taken as affording accurate indices to those occurring normally. Had Sachs had any practical experience of tropical conditions, he could hardly have seriously entertained the idea that the power of movement possessed by the leaves of *Mimosa pudica* has been evolved in connection with the protection which it provides against injuries from hailstorms!

THE

CAUSES OF FLUCTUATIONS IN TURGESCENCE

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CHAPTER I

The essential nature of turgescence in vegetable tissues, the causes giving rise to fluctuations in it, and the various effects which the latter may produce

As all the massive movements occurring in the higher plants, and which are ordinarily ascribed to their irritable properties, are directly dependent on variations in turgidity, it seems to be desirable at the outset briefly to consider certain points regarding the nature and causes of the latter condition

Turgidity is a condition in vegetable tissues in which they contain a greater amount of liquid than that sufficing for their simple saturation In other words, turgid tissues contain more liquid than they are capable of accommodating as the result of their passive physical capacity. The excess of liquid content is the result of the presence of osmotic materials within the tissue elements, and its retention must necessarily give rise to certain effects in these, to an increase in size, to elevation of conditions of pressure, or to both of these combined in various proportions In the case of free protoplasts simple increase in size will occur, and in most tissues increased intracellular pressure will arise in those cases where the cell walls are rigid either intrinsically or from their relations to neighbouring parts, and varying combinations of increased size and increased intracellular pressure where the cell walls are extensible and elastic

In the great majority of cases turgidity in vegetable tissues is essentially dependent on their continued vitality, but at the same time the occurrence of cases in which we find it existing in the highest degree after the death or even entire removal of the protoplasm show that it cannot be directly caused by the latter There is no direct relation between turgidity and the presence of living protoplasm in the turgid elements but yet living protoplasm is necessary in order to the development of turgidity, as it is due to the presence of products of protoplastic activities that the latter arises The condition which holds a direct causal relation to turgidity is the presence of osmotic materials within the protoplasm or cell sap, and these materials are the products of the functional activities of the protoplasm Whether the actual presence of living protoplasm is necessary or unnecessary to the maintenance of turgidity in a tissue is determined

by the nature and amount of the products to which its osmotic properties are due. Where the former are unstable, the cessation or alteration of protoplasmic activity will at once give rise to corresponding changes in the degree of turgidity; where they are stable and present in considerable quantity, turgidity may remain for long, inappreciably affected by death or even complete absence of protoplasm. So long as the osmotic materials which are the direct cause of turgescence are present, the latter will persist under conditions of sufficient water-supply, &c., whether protoplasm be present or absent, and no action of living protoplasts, unless affecting the stock of osmotic materials, can produce any effect on the turgescence of cells.

It may perhaps have been observed that the statement in regard to the effects of turgescence on tissues is a qualified one. The qualification is necessary, because it does not invariably happen that turgescence of the protoplasts of a tissue implies turgescence of the latter as a whole. So long as any protoplast retains its vitality, so long as it continues to exercise its functional activities, it appears normally to be more or less turgid, and the coincidence of protoplastic and cellular turgescence, which we find constantly prevailing in most tissues, is due to the relation which the protoplasts bear to the cell-cavities within which they are situated, and to the fact that even minimal normal turgescence in the former implies a certain amount of active internal pressure in the latter. In any case turgescence is due to the presence of certain products of protoplasmic activity, but so long as they are confined to the interior of the protoplasm, either diffusedly or within accumulations of cell-sap, and the protoplasts are situated within cavities with rigid walls, it is clear that various degrees of protoplastic turgescence may be present without any coincident turgescence of the cells as a whole, and that depression of protoplastic turgescence below a certain degree must give rise to phenomena of natural plasmolysis. The fall in turgescence in the protoplasts implies a corresponding diminution in their bulk, and as the cell-walls are rigid this must tend to a separation of the protoplasm from them. In such cases we have plasmolytic phenomena arising from intrinsic causes, whilst in experimental plasmolysis they are due to extrinsic ones; in artificial plasmolysis the exosmotic property of the medium is raised; in natural plasmolysis the endosmotic properties of the protoplasts are lowered.

In the great majority of cases, however, no such phenomena present themselves under normal circumstances, and even minimal protoplastic turgescence implies a certain degree of turgescence of the tissue as a whole. The interior of the cell-walls is thus constantly subjected to a certain amount of pressure, which may or may not be accompanied by correspondingly active distention of the cell-cavities. The actual degree of tension present at different times, however, varies greatly, the variations being determined by two perfectly distinct sets of factors—factors telling on the absorptive and retentive properties of the cell contents, and factors affecting the supply of water available for absorption and retention, or causing variations in the conditions of external pressure to which the cells are exposed. The former are directly related to the functional activities of the protoplasts; the latter to the general loss and supply of fluid dependent on atmospheric and telluric conditions, to conditions affecting the water-conducting elements of the tissues, or to conditions determining local alterations in pressure in the absorptive tissues themselves.

According to the relations which these two sets of factors bear to one another at different times, variations in the degree of turgescence of the tissues must necessarily be

established Where conditions favouring the formation of endosmotic products by the protoplasts are present coincidently with conditions implying abundant general supply and small general loss, and in the absence of any special causes for active local filtration, turgescence will naturally attain its maximum, where active formation of endosmotic materials coincides with conditions causing deficient supply or excessive loss of fluid, the result in any individual case will be determined by the degree to which each of the opposed sets of factors happens to prevail, and, where a small formation of endosmotic materials and conditions favouring loss or obstructing supply of fluid occur coincidently, minimal degrees of turgescence will naturally present themselves

The variations in turgescence due to the interaction of these various factors must necessarily give rise to various ultimate results according to the nature of the tissue in which they occur. In the cases of tissues in which the conditions for the occurrence of natural plasmolysis occur, varying degrees of contact or separation between the protoplasts and the cell walls will be present, which may be accompanied by conspicuous alterations in colour, especially where the protoplasts include coloured contents In other cases varying degrees of intracellular pressure will constantly prevail which may or may not be accompanied by corresponding variations in bulk of the tissue Where the cell walls are rigid, either intrinsically or from their relations to neighbouring parts, variations in intracellular pressure alone will be present, where they are extensile and free to extend, variations in size will accompany this It is only in the latter case that variations in degree of turgidity can give rise to conspicuous massive movements, and it does not, of course, follow that such should invariably present themselves even under such conditions Variations in the size of the constituent elements of a tissue may result in mere general increase or decrease of its bulk, and it is only where variations in turgidity affect opposed masses of tissue in unlike degree that massive movements will accompany them.

Mere variations in protoplastic turgidity may give rise to very conspicuous changes in the colour of masses of tissue, variations in the turgidity of the tissue elements as a whole, in cases where the cell walls are rigid, may cause appreciable variation in consistence, but cannot serve to induce appreciable variations in bulk or massive movements, variations in turgidity of entire tissues with extensile and elastic cell walls will cause variations in bulk which may or may not be accompanied by conspicuous movements according to their distribution

Fluctuations in turgidity are then, under certain circumstances, efficient in giving rise to massive movements in vegetable organisms, and may themselves be caused either by variations in the nature and amount of the products of protoplastic activity, or in conditions of supply and loss of fluid, and the question next arises, are they the only efficient agents in producing this result, or may the active exercise of contractile function not be one also, as, according to ordinarily accepted opinion, it may actually be?

So far as protoplasts are concerned, it is readily conceivable that active contraction may determine alterations in turgescence, and therefore in bulk, by causing the discharge of fluids included within their substance, but the question which we have to deal with is, how far is mere protoplastic contraction likely to be efficient in giving rise to alterations in the turgescence of cells? In considering this we have in the first place to bear in mind that, in so far as the active protoplasm is concerned, we have unequivocal evidence that contraction does not imply any appreciable alteration in bulk, but mere change in form, and that therefore contraction of a protoplast situated within a cell cavity

does not in itself determine any appreciable diminution in the mass of contents of the latter, but at the utmost a mere rearrangement of them. Active contraction will give rise to increased pressure in fluids contained within the substance of the contracting protoplast, but as these are relatively incompressible, the utmost that this is calculated to give rise to is a mere redistribution, a certain amount of fluid escaping from the interior of the protoplasm and accumulating between it and the cell-wall in plasmolytic fashion. In so far as alterations in the mass of cell-contents are concerned, a protoplast contracting within a cell is practically the parallel of a mass of muscle contracting within a closed vessel of water. The distribution of the muscular mass and of the surrounding water is altered, owing to the change of form occurring in the former on contraction, but the total bulk of content of the vessel remains practically unaltered.

Mere protoplastic contraction being thus insufficient in itself to give rise to diminished turgescence in cells, we have next to consider how far we have any reason to believe that any redistribution of the cell-contents accompanying it may be capable of doing so. Were turgescence in cells necessarily dependent on the presence of fluids included within the substance of the protoplasm, there would be good grounds for supposing that any discharge of these from the latter might lead to diminished turgescence; but as we know that turgescence is directly related to the products of protoplasmic activity and not to protoplasm itself, and that it may be present in high degree apart from the presence of any living protoplasm whatever, we have no grounds for regarding any mere redistribution of the cell-contents, apart from alterations in their osmotic properties, as efficient causes for alterations in cell-turgescence.

If contraction of the protoplasts implied increased pressure on the exterior of the cell-walls, or were necessarily accompanied by change in osmotic properties of the cell-contents, it might well be accompanied by diminished turgescence; but as it certainly cannot lead to the former, and as there is no evidence that it is necessarily associated with the latter, we are justified in regarding it as incapable of affecting cell-turgescence either directly or indirectly. The essential factors which determine the normal fluctuations in turgescence in vegetable cells are alterations in the osmotic properties of their contents and alterations in the conditions regulating general supply and loss of fluid or local filtration; and it does not appear that protoplastic contraction *per se* is capable of producing such changes.

Because conspicuous massive movements occur much more frequently in the organisms of the higher animals than in those of the higher plants, it has been assumed that the mechanism whereby they are produced in the former must necessarily be that which causes them in the latter; but this is of course no matter of logical necessity. Movements in an organism may be arrived at by two perfectly distinct paths—either by means of alterations in form or alterations in bulk of its constituent elements; in the case of the higher animals the former, and in the case of the higher plants the latter, is that which has been followed.

The lines which evolution has pursued in the animal and vegetal series are divergent; in the former contractile and, in association with this, irritable function; and in the latter assimilatory function has been progressively highly specialised. The higher plants, owing to their great superficial extension and highly evolved assimilatory capacity, are enabled to obtain sufficient nutritive materials from those supplies which are generally diffused throughout their environment; consequently any special means for bringing them in condensed and massive form into immediate relation to the organism are unnecessary. In the case

of the higher animals, dependent as they are on supplies of concentrated nutritive materials, such means are essential The end to be attained in both cases is a due supply of nutritive material to make good the constant waste to which living protoplasm is subject in the exercise of its functional properties, in the one case this has been attained by great specialisation of assimilatory function and great extension of surface, in the other by great specialisation of contractile and irritable function Even the most indifferent protoplasm possesses a certain amount of contractile function, but in tracing the course of evolution along the animal and vegetal series of organisms we find that, whilst in the former this has become more and more highly specialised, in the latter it has remained in relative abeyance, while assimilatory power has become predominant, so that it would be just as surprising and anomalous to find any of the higher plants exhibiting phenomena implying the presence of highly specialised contractile apparatus as to find any of the higher animals capable of supplying their nutritional requirements from purely inorganic sources

Both on *à priori* grounds and in the light of abundant positive evidence there is thus good reason to believe that massive movements in the higher plants are not related to the exercise of contractile function, but to assimilatory function as affecting the osmotic properties of the tissues, or to purely physical causes influencing general or local supply and loss of fluid

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CHAPTER II.

Turgidity as distinguished from simple saturation

It is not difficult to adduce evidence showing that turgescence is distinct from mere saturation of tissues, but perhaps the most striking proof is that which is afforded by the phenomena presenting themselves in connection with the exposure of many succulent tissues to the action of anæsthetics The demonstration is peculiarly striking in such cases, because the materials on which the turgescence of the tissue depends are unstable in constitution and are not accumulated in any considerable amount, so that any depression of the functional activities to which they owe their origin is at once followed by a discharge of fluid from the cells, and because, as Dubois has pointed out,* the area of the intercellular spaces is too small to accommodate the masses of it which escape, so that free exudation takes place upon the surface through the stomatic orifices The following experiments illustrate the nature of the phenomena presenting themselves in the case of various common succulents —

A —Kalanchoe laciniata

Experiment I—A leaf weighing 6 54 grammes was set in a chloroform chamber at 10 9 A M A certain degree of darkening in its colour and visible exudation of minute drops of fluid upon the surface were recognisable at 10 17 A M The exudation advanced rapidly, and at 12 30 P M the leaf had become somewhat flaccid and had acquired a

* Mecanisme de l action de Anesthés ques Dr R Dubois Revue Générale des Sciences September 1891 p 561

brownish olive tint. At this time it weighed 5·73 grammes, which, as the fluid of the exudation is practically of the same specific gravity as water, indicated a loss of 0·81*c.c.* of fluid. It was returned to the chamber, and on the following morning it was quite flaccid and weighed only 5·42 grammes, corresponding to a total loss of 1·12*c.c.* of fluid during the course of the experiment.

Experiment II.—A leaf weighing 8·72 grammes was set in a chloroform-chamber. Abundant exudation appeared on the surface within five minutes, and, after six minutes' exposure, large pools of fluid had already formed at some points. It was now gently wiped, and when weighed was found to be only 7·62 grammes. Having been thoroughly washed, it was next set in a common moist chamber, with the cut extremity of the petiole immersed in water. Active exudation continued to occur, and four and a half hours after the beginning of the experiment it was quite flaccid, of a dull, yellowish, olive colour and weighed only 6·67 grammes, equivalent to a total loss of 2·05*c.c.* of fluid, and to a loss of 0·95 after removal from the chloroform-chamber and subjection to the influence of a saturated atmosphere and free supply of water. It was returned to the moist chamber, and on the following morning was found to have sustained an additional loss of 0 34 of fluid.

Experiment III.—A leaf weighing 7·46 grammes was placed in a chloroform-chamber for two minutes and then transferred to a simple moist one, with the cut end of the petiole immersed in water. In three minutes from the beginning of the experiment visible exudation was present, and three hours later the surface was everywhere conspicuously moist, and at one point there was a small pool of fluid. On the following morning it had quite recovered and weighed 7·52 grammes. In this case we have an example of the results following mere temporary depression of protoplasmic activity, as in the two previous ones we had examples of those attending its complete abolition.

Experiment IV.—Two leaves, neither of them being very turgid, were set in a chloroform-chamber. At the end of three hours' exposure they were both quite flaccid and discoloured. The loss in weight in one (*a*) amounted to 0·81 grammes and in the other (*b*) to 1·02 grammes. They were now set in a common moist chamber, (*a*) being totally immersed in water, and (*b*) being set with the cut end of the petiole immersed. On the following morning (*a*) showed a farther loss of 0·33 grammes and (*b*) of 0·36 grammes, but as (*b*) was originally heavier than (*a*) by 1·33 grammes, the relative loss in the latter, although totally submerged in water, was greater than that in (*b*), which was only subjected to the influence of a saturated atmosphere.

Experiment V.—A leaf, weighing 5·12 grammes, set in a chloroform-chamber, began to show visible exudation in the course of six minutes, and at the close of ten minutes had discharged large pools of fluid. It was now removed and carefully dried, and on being weighed showed a loss of 0 28 grammes. It was next at once submerged in water, and on the following morning was quite flaccid, of a yellowish colour, and showed an additional loss in weight of 0·74 grammes. This conclusively shows that complete submersion produces no appreciable effect on the loss of fluid attending the action of anæsthetics on living tissues; for the total loss of weight here amounted to nearly 20 per cent. of the original weight of the leaf, which is much higher than that which often occurs where the tissues are not submerged.

Experiment VI—Two leaves, weighing together 36 grammes, were set in a collecting glass funnel over a receiver in a chloroform chamber On the following day they weighed 32 01 grammes, and a considerable quantity of a yellowish strongly acid fluid, with a specific gravity of 1030, had accumulated in the receiver They remained for twenty four hours longer in the chamber, and at the end of the experiment had sustained a total loss in weight of 4 86 grammes, or 13 5 per cent

Experiment VII—A large leaf, weighing 88 grammes, was suspended free over a collecting funnel, with a view, as far as possible, to avoid maceration of the tissues by the exudation, and set in a chloroform chamber It showed the usual phenomena of free exudation and change of colour, and ultimately lost 14 09 per cent of its original weight The strongly acid, yellowish fluid which collected in the receiver had a specific gravity of 1000

The amount of free exudation taking place in leaves of this plant, and probably of other species also, varies greatly with their age Young leaves yield much less and consequently sustain much less loss in weight than old ones, this being no doubt partly due to the intercellular spaces in the former being relatively considerably larger and affording more accommodation for the fluid on its escape from the interior of the cells

Experiment VIII—A leaf set in an alcohol chamber began to sweat within twenty three minutes, and in the course of three hours had exuded large pools of fluid On the following day it was of a yellowish olive colour, dryish and brittle in texture, and showed a loss of 25 06 per cent in total weight

B —Bryophyllum calycinum

Experiment I—A leaf, weighing 6 44 grammes, was placed in a chloroform chamber Within the course of twenty minutes the under surface had assumed a darker green tint than it had originally, due to displacement of air from the intercellular spaces and its substitution by liquid escaping from the interior of the cells, and at the same time free exudation appeared on the surface in the form of minute drops situated at definite points along the margins A little later exudation also manifested itself over the upper surface generally, here, however, at no particular points, but merely showing a tendency to distribution over the course of the veins Two hours after the beginning of the experiment, the leaf was throughout of a pale yellow colour and had lost 0 13 grammes in weight The relatively small loss of weight and the rapidity of complete discolouration characterising this experiment as compared with those in which *Kalanchoe* leaves were subjected to similar treatment are doubtless to be accounted for as the result of the presence of a relatively extensive intercellular system, which on the one hand afforded comparatively large accommodation for the liquid escaping from the interior of the cells, and on the other brought the latter more readily into relation to the anæsthetic

C —Euphorbia antiquorum

Experiment I—A shoot, weighing 11 26 grammes, was set in a chloroform chamber Within an hour and a half the entire uncut surfaces came to present a peculiar greyish tint, due to the exudation of minute drops of latex into all the depressions in

which the sparsely distributed stomata are present. Only a little watery fluid had escaped at this time, and that solely from the cut extremity of the shoot. On the following morning the uncut surfaces were universally coated by a dry, readily detached, chalky white layer of concrete latex. Very little watery cell-sap could have escaped, as, even after the dry latex had all been carefully rubbed off, the shoot showed a loss of only 0·41 grammes in weight. The cut surface of the pith was, however, slightly depressed, and any section or slight pressure of the epidermis of the intact surfaces was followed by abundant exudation of clear fluid. Microscopical sections of the tissues showed the ramified milk tubes in a more or less shrunken condition, with their walls often thrown into longitudinal wrinkles, giving them a finely striate appearance, and their abundantly nucleated protoplasmic lining contracted. The wrinkling of the tubes and the recession of the protoplasm from the walls are phenomena which are no doubt to be ascribed to the action of the reagents employed in staining and mounting the preparations; but the entire results of the experiment clearly show that the high state of turgescence normally present in the laticiferous system in such cases is no mere passive engorgement due to extraneous pressure exerted by surrounding turgid tissue elements, as Sachs seems to imply.* For, were it due to any such agency, exposure to anæsthetic influences ought certainly not to have given rise to any exudation of latex, seeing that its tendency is to give rise to diminished turgescence generally, and therefore to diminished pressure on the milk tubes. The fact that the tubes are provided with a continuous protoplasmic lining (plate III. fig. 1) is in itself sufficient to indicate that the conditions of turgescence within them must be influenced by intrinsic agencies, and the fact that exudation of latex precedes that of exudation of cell-sap would appear to imply that such agencies are really the main determinant of the extremely high turgescence which normally prevails. What would appear to be the only satisfactory explanation of the phenomena is that both the laticiferous tubes and the other living tissue elements are in a state of active turgescence, but that the turgidity in the former is higher than that in the latter, so that, on the general depression of functional activity incident on the action of an anæsthetic, latex escapes more quickly than common cell-sap, and, occupying the intercellular spaces and concreting when it escapes from the stomatic orifices, prevents the free exudation of the latter. The results of the experiment further show that, in any continuous system of tubes of this nature, turgescence must be interrupted at any points where the functional activity of the protoplasm has been depressed or abolished, such points constituting sites of localised leakage from the system.

In the case of tissues like those employed in the above experiments, the demonstration of the difference between mere saturation and turgescence is rendered particularly plain, owing to the abundant free exudation of fluid which accompanies anæsthesia; but almost equally striking demonstrations are forthcoming in cases where we employ tissues in which the cell-sap contains coloured matters in solution, as the escape of these from the interior of the cell-cavities gives rise to striking changes in appearance, especially in the case of parti-coloured leaves, such as those of many Begonias, &c.

The following experiments illustrate the nature of the phenomena in such cases:—

Experiment I.—A leaf of *Begonia rex*, weighing 1·44 grammes, was set in a chloroform-chamber. The upper surface of the leaf was dull green at the margins and centre,

* Vorlesung, XI. s. 206.

and silvery grey over the intervening areas, the lower one dull red at the margins and pale green with red veins centrally Within half an hour very conspicuous changes in colour had occurred, the green originally present in some parts having almost entirely disappeared and been replaced by diffuse dull red and grey, and the tissues had at the same time partially collapsed, owing to commencing flaccidity Three hours after the *beginning of the experiment the leaf was quite flaccid*, the tissues throughout being translucent and evidently soaked with fluid A mere trace of free exudation had, however, occurred, so that the loss in weight amounted to only 0 04 grammes The disappearance of the green colour originally present in some parts of the surface was no doubt partly due to yellowing of the chlorophyll under the influence of the changes in the tissue incident on the action of the chloroform vapour, but to a much greater extent to the escape and general diffusion of the red colouring matter normally limited to the interior of the cells in certain areas of the inferior surface

Experiment II—A leaf of *Begonia hernandaefolia* was set in a chloroform chamber The leaves in this species are uniformly dull green above and dull red beneath The leaf very rapidly became flaccid, and at the same time the upper surface became diffusedly reddened, due to escape of the coloured fluid from the cells of the lower surface and its general diffusion through the intercellular spaces

Experiment III—A leaf of *Begonia rex*, coloured like that employed in the first experiment, was set in a chloroform chamber Within one quarter of an hour the margins of the upper surface had begun to redden, and shortly afterwards the entire surface gradually became diffusedly red, the leaf at the same time becoming flaccid and collapsed As in the previous experiments, the entire tissue became translucent and soaked and the surfaces moist, but there was no massive discharge of liquid

Experiment IV—A leaf of *Begonia rex*, coloured like the former ones, was set in an alcohol chamber Within twenty minutes traces of reddening appeared in patches on the margins of the upper surface, and at the close of an hour the whole of the upper surface was irregularly blotched with patches of reddish and pale emerald green On the following day the leaf was moist, translucent, red at the margins and centre, and reddish green in the intermediate, originally grey, area of the upper surface The colouring was alike throughout the entire thickness of the lamina Flaccidity did not set in so rapidly or become so highly developed as in the cases in which chloroform was employed, the differences in this respect and in coloration being no doubt due to the fact that whilst chloroform has no affinity for water and no appreciable solvent power for chlorophyll, alcohol is highly endowed with such properties, so that under its influence we have both diffusion of the chlorophyll green and less accumulation of water in the tissues generally The red colour of the cell sap in these cases is apparently unaffected by the changes accompanying anæsthesia, a phenomenon contrasting strongly with what we find occurring in the case of the colour of red petaline tissues under similar circumstances, and no doubt connected with the high permanent acidity of the fluid

Whilst the changes occurring in the living elements of the tissues under the influence of anæsthetics lead to a diminution in their retentive power for fluids, and a consequent loss of turgidity, the water conducting power of the dead elements of the wood remains

entirely unaffected. That this is the case is shown by the results of the following experiments:—

Experiment I.—A leaf of *Cassia sumatrana* was taken and its three distal pairs of pinnæ, together with the corresponding portion of the rachis, were securely luted into a test tube through a perforated and paraffined cork. The leaf was now set with the freshly divided lower extremity in a vessel of water, and the entire apparatus was introduced into a large chloroform-chamber. Three hours later the parts of the leaf which were exposed to the chloroform were quite flaccid, whilst the protected ones remained quite green and turgid. The leaf was now removed from the chloroform-chamber, and, the test tube having been taken off, it was set in a simple moist chamber. On the following day the portion which had been protected remained as before, with the rachis and pinnæ quite green and the latter in a state of full expansion, whilst the whole of the rest of the leaf was of a brownish olive colour and with the pinnæ absolutely flaccid.

Experiment II.—A mature leaf of *Cassia sumatrana*, with the four distal pairs of pinnæ and the corresponding portion of the rachis protected as in the previous experiment, was set in a chloroform-chamber. At the close of three hours the exposed portions were of a dull olive green colour and the pinnæ were very limp, whilst the protected portions remained in their original state. The leaf was now removed from the chamber, the test tube being taken off, and was set in the open laboratory. On the following day the portions which had been exposed to the chloroform were of a dull brownish olive, whilst all those which had been protected were quite fresh, green, and turgid. In a check leaf, which had been set in the open laboratory without water at the same time as the previous one, the pinnæ were all dry and extremely and rigidly depressed, so that it could not have been any conditions of atmospheric humidity which caused the persistent greenness and turgidity of the protected portions of the other.

Experiment III.—A leaf of *Cassia sumatrana* was taken, and the lower extremity of the petiole was freshly divided subaqueously. Both the basal and the distal portions were now protected and the central portion was exposed to the action of chloroform for some time. It was then removed and set in a moist chamber with the base of the petiole luted into a bottle of water. On the following day the portion of the rachis which had been exposed to the chloroform was of a brownish colour and studded with numerous drops of brown exudation, and the corresponding pinnæ were brown, moist, and flaccid; while the protected portions both basal and distal were quite green and turgid and showed no traces of exudation.

Experiment IV.—A young green shoot of *Cassia sumatrana* bearing several leaves was set in a bottle of water. The submerged end of the axis was now freshly cut, so as to present a fresh absorptive surface, and the mouth of the bottle was carefully luted. The apparatus was next set for a short time in a chloroform-chamber, and was then removed and transferred to a common hermetically closed one. Visible exudation of fluid presently occurred on the axis, rachises and petioles, and the pinnæ first partially assumed the normal nocturnal position and then became quite flaccid and olive-brown.

On the following day the drops of fluid on the axis, rachises and petioles had assumed a dark brown colour, which fact, as well as their entire absence from the surfaces of the pinnæ, showed that they were due to exudation and not to surface condensation.

Experiment V.—A shoot of *Cassia sumatrana* set as in the previous experiment. In a little over an hour visible exudation had set in in the axis, rachises and petioles. At this time there was no evidence of change of colour in the pinnæ, but they had in great part assumed their nocturnal positions of depression, convergence, and rotation according to their respective ages, and that the phenomenon was not a simple one of general flaccidity was shown by the fact that in those leaves which, in introducing the shoot into the chamber, had been reversed, the pinnæ, in place of being depressed below the plane of the petiole, were elevated above it. Ultimately general flaccidity and discolouration occurred, accompanied by conspicuous exudation of drops of fluid on the axis and rachises. The discolouration and exudation were sharply limited to those portions of the specimen which had been directly exposed to the chloroform, the base of the axis and the lower part of the lowest petiole which had been protected by the luting remaining quite green, turgid, and devoid of any drops of fluid.

The phenomenon of free exudation on the surface of the axis in such experiments presents itself only so long as the latter is young and has not yet become clothed by any corky strata, in other words, so long as there are stomatic orifices present permitting of the escape of fluid from the dense tissue beneath. So long as it does occur, it is, of course, simply a parallel to the general exudation occurring from the leaves of plants like *Kalanchoe* under similar conditions. The fact of general loss of turgescence throughout the leaves is, in the absence of soluble colouring materials and with the presence of an extensive intercellular area, indicated only by the flaccidity and saturation of the tissues, and the special value of this set of experiments lies in the demonstration afforded by some of them that the capacities of the water conducting system remain entirely unaffected under conditions abolishing the turgescence of tissues in which the active retention of fluid is dependent on the continuous exercise of protoplasmic function, and that the action of anæsthetics like chloroform is a purely localised one, confined solely to the protoplasts which are directly exposed to it, and not leading to any propagation of the depression or abolition of functional activity from the protoplasts so situated to those which are protected from the direct action of the anæsthetic.

The phenomena attending the action of anæsthetics on vegetable tissues are not peculiar, but, save in certain exceptional cases to be presently alluded to, occur whenever protoplasmic function is depressed or abolished in tissues whose turgescence is dependent on the presence of living protoplasm. This comes out very clearly from the results of the following experiments:—

Experiment I.—A leaf of *Kalanchoe*, weighing 12·9 grammes was immersed for about one minute in water at a temperature of 60°*C*, and then gently wiped dry and placed in a hermetically closed chamber. It soon began to exude drops of liquid, which within three hours had accumulated in large pools, the colour of the leaf having at the same time begun to show a yellowish tint. It now weighed 11·2 grammes corresponding to a loss of 1·7 *c c* of fluid. Discharge continued to occur, and on the following morning the weight was only 10·4 grammes, indicating a loss of 2·5 *c c* of fluid and 19·5 per cent of total weight.

Experiment II.—A leaf of *Kalanchoe*, weighing 11·6 grammes, was immersed for half a minute in water at a temperature of 90°*C.*, and then, after being gently dried, set in a hermetically closed chamber. Visible exudation began to appear on the surface within five minutes, and within four hours it had assumed a yellowish olive colour and weighed only 10·1 grammes. On the following morning it had lost 0·4 grammes more, giving a total loss of 1·9*c.c.* of fluid, or 16 per cent. of total weight.

Just as in the case of leaves treated by exposure to chloroform, the amount of loss of fluid taking place from the tissues varies according to the time of year, presumably in relation to the age of the leaf and the area presented by the intercellular spaces, or to the precise nature of the osmotic products present in the cell-sap at different seasons. For example, whilst in the two previous experiments, which were conducted in January, when the leaves are in a dormant condition as regards growth, the losses in weight amounted respectively to 19·3 and 16·3 per cent. of the total, whilst in one carried out in the end of May the total loss amounted to only 4·01 per cent.

Experiment III.—A leaf of *Cassia sumatrana* with eleven pairs of pinnae was taken, and the centrally situated pair and the corresponding portion of the rachis were dipped into boiling water. The boiled pinnæ became flaccid at once and dropped vertically downwards from the petiole, with their upper surface looking directly outwards. The base of the petiole was now freshly divided under water, and the leaf, along with a check one, set to stand in a bottle of water in the open laboratory. The boiled pinnæ had at once assumed a yellowish olive tint and presently became distinctly yellow, the colour being quite distinct from that following prolonged exposure to chloroform. A certain amount of tendency towards the assumption of the normal nocturnal position manifested itself in the pair of pinnæ immediately beyond the boiled portion of the petiole, but this had completely disappeared within the course of three hours. On the following day the boiled portions of the leaf were yellowish-brown and dry, whilst the proximal and distal portions were green and turgid. The pinnæ of the distal portion were, however, more or less in the nocturnal position, this being, no doubt, due to the fact that, whilst the conduction of water through the wood remained unimpaired, the dead superficial tissues of the boiled portions of the leaf presented a site of abnormally excessive evaporative loss, as indicated by their dry condition.

Experiment IV.—A leaf of *Cassia sumatrana*, like the preceding one, was taken and the fourth and fifth pairs of pinnæ with the corresponding portion of the rachis were dipped into boiling water. Immediate and total depression of these pinnæ occurred, and was soon followed by a partial assumption of the nocturnal position in the sixth pair. The base of the petiole was now freshly divided under water and luted into a water-bottle in a hermetically sealed chamber. The sixth pair of pinnæ rapidly resumed the fully expanded condition, and yellowing of the fifth and sixth pairs and of the corresponding portion of the rachis soon manifested themselves, the surface of the rachis at the same time becoming studded by an exudation of drops of fluid. On the following day the boiled pinnæ were quite flaccid, moist and yellowish-brown, and the corresponding portion of the rachis was covered by large drops of brownish fluid, while all the rest of the leaf was turgid, bright green and fully expanded. It was now removed from the chamber and set in the open laboratory, and, in a short time, the drops of exudation disappeared from the boiled portion of the rachis and simultaneously the distal intact

pinnæ began to show rotation and depression, whilst the proximal ones retained the fully developed diurnal position unaltered The fact that boiling the tissues in such cases leaves their conducting power for water unimpaired, whilst reducing their retentive power, could hardly be more clearly demonstrated than it is in the results of this experiment by the phenomena of exudation in the boiled areas and full expansion of the distal intact ones whilst the leaf remained in a moist atmosphere, and of disappearance of exudation and partial assumption of the nocturnal position by the same pinnæ when the leaf was exposed to free evaporative loss On the following day the level of the water in the bottle had sunk so much that only the tip of the petiole remained immersed The boiled portions of the leaf were dry and brown, the others were green and turgid, but somewhat inclined towards the nocturnal position The leaf was now returned to a hermetically closed chamber, and on the following day exudation had reappeared on the boiled portion of the rachis and the intact pinnæ were once more in a condition of full expansion

Experiment V—Two leaves of *Cassia sumatrana* were taken, the one, *a*, having seven pairs of pinnæ, the other, which was somewhat larger, only six and a half pairs The third pair of pinnæ and the corresponding portion of the rachis of *a* were immersed in boiling water, the treatment causing almost immediate browning and flaccidity of the immersed tissues, and temporary drooping, with more or less assumption of the nocturnal position in the pinnæ beyond the point of immersion The bases of the petioles of both leaves were now freshly divided under water and then securely luted into water bottles, the levels of the water in the latter being at the same time accurately marked The leaves stood side by side in the open laboratory until the following day, when both were found to be alike turgid, save the boiled portions of *a*, which, as usual with exposed portions of tissue after similar treatment, were brown, dry, and drooping The amount of water which had been absorbed during the interval in both cases was 3*c c*

Experiment VI—A large leaf of *Cassia alata* was taken, and all but the five distal pairs of pinnæ were cut off The lower part of the petiole was then plunged into boiling water for half a minute, and, its extremity having been cut off subaqueously, was luted into a water bottle The apparatus was then set in a sealed chamber containing a vessel of strong sulphuric acid The level of the water in the bottle began at once to descend visibly On the following day that part of the boiled portion of the petiole which was above the water was of a brown colour and coated with drops of brown fluid The pinnæ at the same time were fully expanded, turgid, bright green and as usual when saturated with fluid, studded marginally with drops of clear liquid The water in the bottle had meantime sunk very considerably On the two following days the pinnæ retained their greenness and turgidity, and at the close of the experiment the quantity of water which had been absorbed amounted to 15*c c*

Experiment VII—A large leaf of *Cassia alata* was taken, the basal pair of pinnæ removed, and the lower four and a half inches of the rachis immersed in boiling water for two minutes The end of the petiole was then freshly cut off under water, and the leaf set in an open water bottle and fixed, so that the lower part only of the boiled portion of the petiole was immersed Visible depression of the level of the water set in at once, and in the course of two hours a loss of 12*c c* had occurred On the following morning an additional loss of 38*c c* was registered, giving a total

of 50*c.c.* In this case about 50*c.c.* had traversed the boiled portion of the petiole within twenty-four hours, for the loss by mere evaporation in a check bottle of water was almost inappreciable during the same period. The nine pairs of pinnæ which had been left on the leaf remained quite green and turgid.

Experiment VIII.—Two leaves of *Cassia alata* were taken, and all the pinnæ save the two terminal pairs were cut off. One specimen was then entirely immersed in boiling water for a minute, and the lower part of the petiole of the other was similarly treated. The extremities of the petioles were then freshly divided under water and set side by side in marked water-bottles. On the following day the water in the bottle containing the wholly boiled specimen showed a loss of 10*c.c.*, and that in the other one of 14*c.c.* The pinnæ in the wholly boiled leaf were quite flaccid, drooping, and brownish, whilst those in the other were fully expanded, green, and turgid. Twenty-four hours later an additional loss of 7*c.c.* was registered in the former and one of 8*c.c.* in the latter specimen. The amount of water absorbed by the wholly dead leaf during the entire course of the experiment was only 5*c.c.* less than that in the case in which the lower part of the petiole alone had been boiled; but in estimating the amount of absorption due to the vital activities of the tissues in the latter it must be borne in mind that the amount of loss due to simple evaporation in it was certainly much less than in the other specimen, in which the retentive power for fluid connected with functional activity had been totally abolished.

Experiment IX.—Two leaves of *Cassia alata*, each bearing eight pairs of pinnæ after the removal of the basal pair, were set side by side in marked water-bottles, the lower part of the petiole having in one case been boiled for two minutes and in the other left intact. Twenty-four hours later the pinnæ of both leaves alike were fully expanded, green and turgid, and the loss of water registered by each bottle was 23*c.c.* The boiled portion of the petiole of the one leaf was quite brown and the cortical parenchyma flaccid. One phenomenon which presented itself in this case was that the absorption of water was primarily more rapid in the specimen in which the lower part of the petiole had been boiled than in that in which it had been left intact, this no doubt being due to the aspiratory action of the gaseous contents of the water-conducting system on contracting under the influence the fall of temperature subsequent to removal from the boiling water.

It appears clear from the previous experiments that the action of heat and chloroform on living vegetable tissues is strictly localised to the parts directly exposed to their influence, and that, even where the exposure results in death, there is no propagation of any effects to protected parts, however close to and continuous with the injured ones they may be. In other words, there is no evidence that the death of the protoplasts in one part produces any appreciable direct results on the well-being of neighbouring but protected parts. The quantity and quality of the water-supply conducted by the vascular tissues remains inappreciably affected by chloroform; and although heat may temporarily affect the former, due to the expansion of the gaseous contents of the conducting system which it induces, the obstruction thus arising is transitory, and this being so, in neither case does the mere loss of turgescence and death of neighbouring parts ordinarily give rise to any appreciable effects. Very different results ensue, as is shown by the next experiment, where the reagent which

is primarily locally applied is readily soluble in water, and therefore liable to be conducted by the stream of fluid traversing the vascular tissues

Experiment X—Two leaves of *Cassia sumatrana* were taken and set with the bases of their petioles immersed in water and subaqueously divided in order to permit of free absorption One of them (*a*) was now along with its water vessel introduced into a beaker containing a little ammonia, the mouth of the beaker being closed by a cork securely luted down and around the rachis, so that whilst the lower portion of the latter and the basal pinnæ were enclosed in the beaker and exposed to the ammonia vapour, the upper portion and the distal pinnæ projected free into the air and had no immediate relation to the reagent The other leaf (*b*) was similarly treated, only in this case the beaker contained chloroform in place of ammonia The pinnæ of (*a*) which were within the beaker rapidly acquired a dark colour, whilst drops of black fluid began to exude from the surface of the rachis, and shortly afterwards similar changes began to manifest themselves in the part of the leaf outside the beaker, the pinnæ drooping and darkening in colour especially along the neighbourhood of their midribs, and exudation beginning to appear on the rachis. Twenty four hours later the leaf was wilted throughout, the pinnæ greatly blackened and the rachis thickly studded with drops of black fluid The portions of (*b*) which were included in the beaker were also very rapidly affected, the pinnæ becoming flaccid and of a brownish olive colour and the rachis exuding drops of pale yellowish fluid, but there was no extension of these changes to the portion of the leaf beyond the cork, the pinnæ retaining their original colour and turgidity and the rachis showing no signs of exudation On the following day the free portions of the leaf remained entirely unaffected, and the pinnæ were fully expanded, turgid and of their original bright green colour, while the petiole, even down to the surface of the cork, showed no signs of any change

Here, in both leaves alike, the tissues which were directly exposed to the influence of the reagent were rapidly killed and rendered flaccid by loss of turgidity, but whilst in one case these changes extended rapidly and completely throughout the entire leaf, in the other there was no propagation of them to the protected parts Both reagents rapidly induce death in tissues directly exposed to their influence, but whilst chloroform is only very slightly soluble in water, ammonia is excessively so, and therefore is readily conveyed to distal areas Such experiments afford no evidence of the transfer of any influences by means of the protoplasmic continuity of the tissues, the complete death of great masses of tissue failing to give rise to any appreciable effects in immediately contiguous parts so long as the water supply of the latter remains unaffected, but they unequivocally show how rapidly changes may be propagated to distal areas by means of alterations in their water supply This is a question which will be recurred to subsequently, and it is merely alluded to here because the phenomena of the experiment appear so clearly to suggest that it is to the water conducting system and not to any system of continuous protoplasts that we must look for an explanation of the propagation of effects from one area to another in the organism of any of the higher plants.

The above experiments have demonstrated very clearly that exposure of vegetable tissues to excessive heat gives rise to effects similar to those which follow their exposure

to the action of anæsthetics, and the next one shows that excessively low temperatures produce the same effect.

Experiment XI.—A large leaf of *Kalanchoe*, weighing 28·75 grammes, was put into a metal box and buried in a mixture of pounded ice and salt. On being removed after an interval of an hour and a quarter it was found to be rigidly frozen, but without visible exudation or change of colour. It was now set in a hermetically closed chamber, and very soon began to sweat visibly. On the following day it had acquired a yellowish tint and was quite flaccid and moist. The weight was now only 24·16 grammes, corresponding to a loss of 4·59*c.c.* of fluid, and on the following day was only 22·55 grammes, giving a total loss of 21·5 per cent. on the original weight. The only difference presented by the phenomena in this case as compared with those occurring in cases of anæsthesia was the primary absence of exudation; but this is readily accounted for if it be taken into account that any liquid entering the intercellular spaces in the initial stages of the experiment must have been frozen as it approached the surface of the leaf, and so have plugged the stomatic orifices.

It is not, however, merely anæsthetics and excessive elevation or depression of temperature which produce such results, for essentially similar ones occur in cases where the tissues are exposed to strong acid or alkaline vapours, to immersion in solutions of corrosive sublimate, or to the influence of electrical currents or discharges.

I have not personally tried any experiments on the action of electrical currents on vegetable tissues, but the accounts which are furnished by Becquerel* regarding the results of his investigations of the subject leave no doubt that they also give rise to a loss of turgescence. He found that, in the case of milky Euphorbias, treatment of the shoots with electrical discharges was followed by a suppression of the discharge of latex on subsequent incision, a phenomenon which can only have been due to loss of turgescence in the milk tubes. When leaves of *Begonia discolor*, which are red on one face and green on the other, were subjected to electrical currents, the red face became sensibly green and the green one red, due to escape of the red fluid from the interior of the cells normally containing it and its diffusion throughout the intercellular spaces of the tissue. He was at first inclined to explain the escape of liquid from the cells as due to rupture of the walls of the latter under the influence of the electricity; but, finding that there was no microscopical evidence of rupture, he ultimately came to the conclusion that the phenomenon was due to alterations in the nature of the cell-sap.

The following experiments illustrate the effects produced by exposure of the tissues to poisonous vapours and solutions:—

Experiment XII.—A leaf of *Kalanchoe*, weighing 10·03 grammes, was set in a carbonic acid chamber. The first result which manifested itself was a certain amount of intensification of the green colour of the tissue, but the surface gradually became moist, and within a quarter of an hour actual exudation of drops of liquid had occurred. On the following day the leaf was of a dull, ochreous brown colour and weighed only 8·9 grammes. It was returned to the chamber, and twenty-four hours later was almost

* "Des Forces Physico-Chimiques." Paris, 1875.

completely flaccid and weighed 8 06 grammes, equivalent to a loss of 19 6 per cent on the original weight and to an exudation of 1 97c c of liquid.

Experiment XIII—A leaf of *Kalanchoe*, weighing 27 93 grammes, was set in a carbonic acid chamber. Visible exudation began within the course of an hour and advanced rapidly, accompanied by collapse of the leaf The reddish colouring along the margins of the lobes was, primarily at all events, intensified, and the rest of the surface gradually became yellowish On the following day the leaf was moist, flaccid, and weighed only 24 61 grammes, indicating a loss of 11 8 per cent.

Experiment XIV—A leaf of *Kalanchoe*, weighing 13 64 grammes, was suspended over water in a carbonic acid chamber. It remained in the chamber for forty eight hours, and at the close of that period was flaccid, of a yellowish olive colour, and weighed only 11 54 grammes, indicating a loss of 15 3 per cent of total weight

Experiment XV—A leaf of *Kalanchoe*, weighing 33 22 grammes, was set in a hydrochloric acid chamber Visible exudation and brightening of the red colour at the margins of the lobes soon appeared On the following day it was flaccid and of a dull yellowish olive colour, and weighed only 28 51 grammes

Experiment XVI—A leaf of *Kalanchoe*, weighing 18 12 grammes, was set in a hydrochloric acid chamber. Visible exudation was present within a quarter of an hour Twenty four hours later it was very moist, quite flaccid, of a yellowish olive colour, and weighed only 15 02 grammes

Experiment XVII—A leaf of *Kalanchoe*, weighing 14 62 grammes, was placed in a nitric acid chamber On the following day it was of a yellowish olive colour with the edges of the lobes strong pink It was not so moist or flaccid as a leaf treated at the same time in a hydrochloric acid chamber, but showed a loss of 15 5 per cent in weight

Experiment XVIII—A leaf of *Kalanchoe*, weighing 13 08 grammes, was set in a nitric acid chamber. Visible exudation occurred within two hours, and on the following day it was perfectly flaccid, of a dull olive with pinkish along the margins of the lobes, and weighed only 10 23 grammes, having lost 21 7 per cent in total weight

Experiment XIX—A leaf of *Kalanchoe*, weighing 14 13 grammes, was set in an osmic acid chamber Blackening of the surface rapidly set in, and on the following day it was coal black and covered by large isolated drops of inky fluid It was not however, flaccid, and only showed a loss of 7 2 per cent in weight, whilst a leaf which had been exposed simultaneously in a nitric acid chamber showed one of 21 7 per cent Twenty four hours later it was still nearly rigid, but had discharged a considerable additional amount of black liquid and only weighed 12 51 grammes

Experiment XX—A leaf of *Kalanchoe*, weighing 15 17 grammes, was set in an osmic acid chamber It began rapidly to blacken at the edges, and at the close of two hours the discolouration had spread inwards considerably, and one or two small drops of black exudation had appeared on the surface of all the lobes save one There

was no general moistening of the surface or any indication of commencing flaccidity. Three hours after the beginning of the experiment it was very greatly blackened, but was still quite rigid and had lost only 0·07 grammes in weight. On the following morning it was perfectly black, but had discharged very little more fluid, the texture remaining quite firm and the weight being 14·64 grammes. Twenty-four hours later, *i.e.*, forty-eight hours from the beginning of the experiment, a certain amount of further exudation had occurred and the weight was 14·13 grammes, the total loss from the beginning of the experiment having only amounted to 6·8 per cent. The slowness and limitation of exudation attending exposure to this reagent as compared with the discharge taking place under the influence of the others is very remarkable. The phenomenon must be due either to some alteration produced in the cell-sap, whereby stable in place of unstable osmotic materials come to be present in it, or more probably to alterations in the protoplasm rendering it less filtrative than it is under ordinary circumstances.

Experiment XXI.—A leaf of *Kalanchoe*, weighing 26·87 grammes, was set in an ammonia chamber. Conspicuous sweating took place in the lobes nearest to the vessel containing the ammonia within the course of five minutes, and the tissues gradually assumed an intense deep green colour. On the following day it was of a very deep olive green. The surface of the leaf was moist, but its texture was not flaccid. Twenty-four hours later the colour remained as before, and the weight was 23·42 grammes, equivalent to a total loss of 12·8 per cent.

Experiment XXII.—A leaf of *Kalanchoe*, weighing 8·7 grammes, was set in a moist ammonia chamber. Within ten minutes it became of a vivid deep green, and had begun to sweat conspicuously. On the following day it was dark green and very moist, but still rigid and smelling strongly of ammonia. The ammonia was removed so as to convert the chamber into a simple moist one and the leaf replaced in it. The weight of the leaf at this time was 8·52 grammes. It was kept under observation for three more days, during which it continued to give off ammonia as indicated by the smell of the water in the chamber, which was renewed daily. The losses in weight for the successive periods of twenty-four hours were 0·88, 0·29, and 0·11 grammes, giving a total loss for the entire experiment of 1·56 grammes, or 17·9 per cent. of weight.

Experiment XXIII.—A leaf of *Kalanchoe*, weighing 29·22 grammes, was immersed for forty minutes in a 2·5 per cent. alcoholic solution of corrosive sublimate. When removed and gently dried, it weighed 29·3 grammes. It was now placed in a moist chamber, and shortly began to sweat actively. On the following day it was partially flaccid, much fluid had been already discharged, and active exudation was still going on. At this time it weighed 26·44 grammes. It continued to discharge fluid, although kept continuously in a sealed moist chamber, for the next eight days, and at the close of that period it was excessively flaccid, of a pale yellowish olive colour, and only weighed 21·03 grammes, corresponding to a total loss of 8·19 grammes, or 28·2 per cent. of weight.

Experiment XXIV.—A leaf of *Kalanchoe*, weighing 12·0 grammes, was immersed in a saturated aqueous solution of corrosive sublimate, the extremity of the petiole being freshly divided after immersion in order to facilitate absorption. Twenty-two hours

later it was removed from the solution and gently wiped dry* It now weighed only 9·53 grammes, indicating a loss of 20·5 per cent of total weight, and was flaccid and of a pale ochreous colour It was next placed in a simple moist chamber, and by the following day had discharged a considerable amount of fluid and weighed only 8·26 grammes It would be hard to find a more striking demonstration of the fact that turgidity is distinct from simple saturation than is afforded by the results of this experiment in which, whilst the leaf was actually submerged in the solution, such a considerable loss of fluid occurred

The most important points which are illustrated by the experimental data in the present chapter are the following —

1st—That turgescence implies saturation of tissue elements including osmotic materials, and must therefore be distinguished from simple saturation

2nd—That where turgescence is dependent on continued vitality, the relations of certain tissue elements to fluids are profoundly altered by conditions which produce no appreciable effect on those of others

3rd—That where turgescence is dependent on continued vitality, its diminution or total abolition may be determined by such varied conditions as exposure to alkaline or acid vapours, to anæsthetics, poisonous substances in solution, extremes of temperature, and electrical currents

4th—That the only other common effect which these different factors produce in the tissues is the ultimate death of their living elements, or, in other words, that depression or abolition of functional activity leads to diminution or disappearance of turgidity But this, taken along with the fact that we have abundant evidence that certain forms of stimulation give rise to increase in cell turgescence, and no unequivocal evidence that any forms of stimulation give rise to its decrease, almost forces us to believe that it is depression and not stimulation of functional activity that is related to any movements which are determined by functional causes and dependent on diminished cell turgescence and this finally leads us to the conclusion already arrived at on independent grounds in the previous chapter, that it is fluctuation in the activity of assimilatory and respiratory function, and not fluctuations in the activity of contractile function, that are essentially related to movements connected with alterations in the turgescence of cellular vegetable tissues

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CHAPTER III

The relation of turgescence to protoplasmic activity

The facts which have been detailed in the preceding chapter might, if taken alone, be regarded as evidence that turgescence is a peculiarity of living tissues and therefore directly and necessarily related to the presence of living protoplasm, and this opinion has

* In all cases in which portions of the petioles were detached in the course of any experiments they were of course carefully preserved and included in any subsequent weighments

to a great degree coloured the various explanations which have been advanced to account for the occurrence of the sudden fluctuations in turgescence on which the movements of masses of vegetable tissues depend. Sachs, for example, affirms that turgescence is essentially due to the great resistance which protoplasm normally presents to the filtrative escape of any liquids which it may have endosmotically acquired, and that any sudden escape of water from a turgescent cell necessarily implies a change in the nature of the protoplasm whereby it readily permits of filtration.* He practically ascribes everything directly to the protoplasm and nothing to the influence of the products of its activity contained within the cell-sap, and by doing so is constrained to endow the protoplasm with certain special properties in order to account for the phenomena which actually occur. In adopting this view he entirely loses sight of the possibility that turgescence may be due to the osmotic properties of the cell-sap overcoming the filtrative facilities provided by the protoplasm, and that loss of turgescence may arise as the result of diminution in the former, and not of any increase in the latter, of these two factors; and when we come to look for any positive evidence tending to a decision of the question, we find that, whilst we can readily trace the occurrence of chemical changes in the cell-sap which may well cause changes in its osmotic properties coinciding with loss in turgescence, we are unable to find any proof of alteration in the filtrative power of the protoplasm save the very phenomenon which it is regarded as giving rise to. If we ascribe turgescence directly to the properties of the protoplasm, we are left to assume that any fluctuations in the former must be accompanied by changes in the latter; but if we ascribe it to the properties of the cell-sap, we can at all events show that loss in turgescence is accompanied by changes in the chemical constitution of the factor. According to the one view, anæsthetics and all the other factors which we have just seen acting as determinants of loss of turgescence must do so simply because they have the common property of increasing the filtrative power of the protoplasm; according to the other, the result is due to alterations in the properties of the cell-sap attending depression and abolition of respiratory and assimilative function in the protoplasm, and of the occurrence of which we have in many cases the clearest chemical evidence.

The conspicuous changes in the colour of common green leaves attending losses in turgescence caused by exposure to injurious media very clearly indicate the occurrence of coincident chemical changes in the contents of the cells; but much more striking evidence is forthcoming where variously coloured floral tissues form the subjects of experiment.

In the case of common leaves the changes in colour accompanying depression and abolition of functional activity (unless induced by media, such as ammonia, which secure the addition of extraneous alkaline constituents to the tissues) are such as to indicate a rise in fixed acidity, the yellowing which takes place being precisely of the character presenting itself in neutral solutions of chlorophyll on the addition of acids. This change in certain cases may be partially ascribed to the addition of extraneous acid during the course of the experiment; but the fact that it manifests itself in cases where chloroform or extremes of temperature are the agents employed shows that no extraneous agency is required to produce it. Fortunately it is not necessary to be satisfied with this chromatic evidence alone, as it is possible to adduce positive proof that depression of functional activity is, in some cases at all events, directly related to an increase in the fixed acidity

* Vorlesungen, XVI. p. 330, XXXVII. p. 798.

of the cell sap This is demonstrated by the following experiments which were originally suggested by a paper, published in the year 1815 in the eleventh volume of the transactions of the Linnean Society, and to which my attention was first directed by my friend Dr David Prain It is entitled "On the Deoxidation of the Leaves of *Cotyledon calycina*" (= *Bryophyllum calycinum*) and in it the author, Dr Heyne, points out that a *conspicuous decrease in the acidity of the tissues (which he ascribes to processes of deoxidation)* takes place during the course of each diurnal period, alternating with a corresponding increase in each nocturnal one *

On testing the leaves of *Kalanchoe laciniata* it was at once ascertained that they exhibited similar phenomena Observations were first instituted during the course of the hot season when transpiratory loss is very active diurnally, and when the amount of fluid escaping on section of the leaves is much smaller in the evening than in the morning, but, in spite of this, it was at once evident that the acidity, and specially the fixed acidity of the evening (and presumably concentrated) sap, was much lower than that of the fluid escaping in the morning (plate III fig 2) Systematic investigation of the subject afforded the following results —

Experiment I—Two leaves of *Kalanchoe* were taken, one, *a*, weighing 16 93 grammes, and the other, *b*, 30 75 grammes In both of them the reaction of the cell sap was highly acid at 10 30 A M when the experiment was begun They were both exposed to direct but broken sunshine beneath a tree, *a* being enclosed in a chloroform chamber, and *b* set with the base of the petiole in water. At 2 P.M *a* weighed 12 2 grammes, was of a pale ochreous olive colour and very flaccid, whilst *b* was bright green and turgid, and weighed 31 38 grammes The sap of *a* was intensely and permanently acid, that of *b* was even at first only faintly acid and only contained a mere trace of permanent acidity

Experiment II—A leaf of *Kalanchoe*, weighing 30 3 grammes, was exposed to direct sunshine apart from water for three hours and a quarter When first set at 10 30 A M, its juice was intensely acid After exposure it weighed 28 48 grammes, and the permanent acidity of the sap was very feeble It was now set with the freshly divided base of the petiole in water, and on the following morning the weight was 28 72 grammes, and the permanent acidity of the sap intense

Experiment III—A leaf of *Kalanchoe*, weighing 30 58 grammes, and with highly acid sap was set with the base of the petiole in water in absolute darkness at 10 30 A M At 1-45 P M the weight had increased to 31 08 grammes, and the acidity of the sap remained apparently unaltered

Experiment IV—Two leaves of *Kalanchoe*, one, *a*, weighing 29 6 grammes, the other, *b*, 23 4 grammes, were set with the bases of the petioles immersed in water The sap in both of them was highly acid in reaction, *a* was exposed to direct sunshine and *b* to absolute darkness for more than three hours At the close of this period *a* was slightly limp, weighed only 27 7 grammes, and on section yielded comparatively little fluid, with a mere trace of fixed acidity, whilst *b* was fully turgid, weighed 23 71 grammes, and yielded an abundance of intensely and permanently acid fluid

* Transactions of the Linnean Society vol. XI p. 213.

Experiment V.—Two leaves of *Kalanchoe* with intensely acid sap were taken at 10-15 A.M. One, *a*, weighed 28·7 grammes; the other, *b*, 28·58 grammes. Both were then set with the bases of their petioles immersed in water, and *a* was exposed to direct sunshine and *b* to absolute darkness for three hours and a half. At the close of this period, *a* weighed only 27·3 grammes, and the acidity, and especially the permanent acidity, of its juice was very greatly diminished in intensity; while *b* weighed 27·87 grammes and yielded fluid of excessively acid reaction. On the following morning the acidity of the sap in both cases was alike and intense. The leaf *b* was now enclosed in a moist chamber and exposed for three hours in absolute darkness to a temperature of 88·7 in order to determine whether the effects following exposure to sunshine were in any appreciable degree determined by heat as distinct from light; but the acidity of the sap remained undiminished at the end of the experiment.

In this case the stimulant ultimately leading to a diminution in the acidity of the cell-sap is evidently light, but in other cases heat comes prominently into play in producing similar results. For example, whenever the temperature remains beneath a certain limit the flowers of *Ipomœa hederacea*, however brilliant the sunlight be, never attain the intense, dusky blue normal to them when in the expanded condition, but retain more or less of the red tint proper to the buds—a phenomenon which, as we shall presently see, is due to a relative excess of acid constituents in the cell-sap. Here temperature is the determinant of decrease in acidity, just as in other cases we find that it is the essential determinant of the increase in turgidity of certain masses of tissue on which the expansion of flowers such as those of *Portulaca grandiflora* is dependent. The flowers of *Portulaca* do not unfold in the brightest sunshine until they have attained a temperature of 70° to 80°F.; and, if only this be provided, expansion takes place in total darkness just in proportion to the rise in temperature. Both heat and light are clearly capable of determining chemical alterations in the nature of the cell-sap and increase in the turgescence of masses of tissue. According to Sachs' theory of the causation of turgescence, in order to account for the phenomena we must assume that in some cases the factors act on the physical properties of the protoplasm, and in others on the chemical nature of the cell-sap; or, in other words, that in some cases they affect the structure and in others the function of the protoplasm. But surely it is more reasonable to assume that both chromatic and motor effects are due to stimulation of the latter only. Such stimulation may well give rise to the formation of products differing from one another in different instances, in some characterised by their reaction and in others by their osmotic properties, and accordingly ultimately determining changes of colour in the one case and movements related to altered turgescence in the other case.

In some cases stimulation of functional activity, whether photic or thermic, leads to decrease and in others to increase in the acidity of the cell-sap and to corresponding changes in the tint of colouring matters which are dissolved in it, the intensity of blue and green colours being related to relative alkalinity and that of red ones to relative acidity. That this is the case is shown by the results of the following experiments:—

Experiment I.—The petals of a flower of *Erythrina stricta*, which are of a brilliant scarlet colour, exposed in a chloroform-chamber almost immediately became of a

permanent pale, dull, brownish pink tint. The flower was now transferred to a carbonic acid chamber in which the petals gradually reddened, and in the course of twenty-four hours they had regained a vivid scarlet colour.

Experiment II.—Petals of the same *Erythrina*, when immersed in absolute alcohol, were at once bleached to a very pale pink, the alcohol at the same time acquiring a very pale, reddish topaz tint, which rapidly reddened in a carbonic acid chamber and became vivid scarlet on the addition of a few drops of glacial acetic acid. Alternate additions of solutions of caustic potash and glacial acetic acid to alcoholic extract which has become scarlet owing to prolonged exposure in a carbonic acid chamber, secure alternating discharge and reformation of the colour.

Experiment III.—A flower of a scarlet variety of *Hibiscus rosa-sinensis* was set in a chloroform-chamber. The colour very rapidly began to become dulled, and within an hour was of a dull maroon red, the corolla at the same time showing the initial stages of collapse. The chloroform was now removed from the chamber and a vessel of glacial acetic acid substituted for it. Collapse of the corolla continued to advance steadily to completion, but at the same time its colour gradually revived and ultimately became once more vivid scarlet.

Experiment IV.—A similar flower of *Hibiscus*, momentarily immersed in boiling water, collapsed at once, the colour at the same time becoming purplish. The water also acquired a purplish hue, due to extraction of pigment and partial bleaching of the corolla. The purplish infusion was rendered bright red by the addition of acids.

Experiment V.—A similar flower placed in a chloroform-chamber gradually underwent the same changes as that in *Experiment III.*

When the colour had become of a deep maroon red, the chloroform was removed and a vessel of fuming nitric acid substituted for it. Restoration of the colour began visibly almost at once, and a vivid scarlet was gradually re-established.

Experiment VI.—A similar flower was enclosed in a metal box and buried in a mixture of ice and salt. After an hour and a half of exposure it was found to be stiffly frozen and of a dull red colour. It was now placed in a simple hermetically closed chamber, and the colour soon passed on to the same deep maroon tint which is developed under exposure to chloroform, flaccidity and collapse also advancing rapidly. On the following day it was quite flaccid and deep maroon. A vessel of glacial acetic acid was now introduced into the chamber, and twenty-four hours later the corolla was once more vivid scarlet.

Experiment VII.—Petals of scarlet *Hibiscus* immersed in absolute alcohol became at once deep purple and yielded a neutral extract of a reddish topaz colour. Treated with acids, this extract became vivid red; and with alkalies dull green, passing on to orange yellow.

Experiment VIII.—A scarlet *Hibiscus* flower was set in a moist ammonia chamber. Purplish black spotting of the corolla began to appear within a minute and extended rapidly. As the blackening extended inwards from the periphery to the centre of the

corolla, the margins gradually assumed an orange tint, and on the following day the flower, although hardly showing any signs of collapse, was of a uniform brownish orange throughout.

Experiment IX.—A flower of scarlet *Hibiscus* in a chloroform-chamber very rapidly collapsed, and at the same time assumed a deep maroon red colour. Immersion of the discoloured petals respectively in dilute acetic acid and in 10 per cent. solution of caustic potash caused them, in the former instance, again to become scarlet; and, in the latter, to turn first dull blue, then dull green, and finally ochreous.

Experiment X.—Two flowers of *Ipomœa hederacea* were placed in a chloroform-chamber. The deep blue portions of the corollas almost immediately began to acquire a violet, and the pale rose of the red parts an ochreous tint. The violet of the blue areas gradually reddened and, at the same time, the texture visibly became moistened. The corollas ultimately collapsed, the originally red area being now ochreous and the originally blue ones dull red.

Experiment XI.—A flower of *Ipomœa hederacea* was set in a moist chloroform-chamber at 10-31 A.M. The blue area of the corolla gradually became first violet and then dull red, and at the same time slowly collapsed.

Experiment XII.—A flower of *Ipomœa hederacea* was set in a moist ammonia-chamber. After three minutes' exposure it had become of a vivid peacock green, which gradually faded to a pale ochre.

The changes in colour in the flowers of *Ipomœa hederacea* under the influence of chloroform are just the reverse of those which normally take place during the expansion, but are the same as those attending the withering of the corollas. Whilst in bud the areas which, during full expansion, are reddish have an ochreous, and those which are deep blue a red colour; and in the fading and faded corollas of the afternoon and night a reversion to the bud colouring takes place. When the dull red faded corollas are treated with acids they become vivid rose colour; and, when treated with alkalis, vivid blue and green, passing on into pale yellow. When the flowers are in bud and in the faded condition, the cell-sap thus evidently contains a relative excess of acid constituents; whilst, when the flower expands under favourable conditions of light, and specially of temperature, these acids are partially neutralised by the manufacture of alkaline products. Stimulation of the functional activities of the tissues in this case gives rise to effects similar to those accompanying it in tissues containing chlorophyll, and precisely the reverse of those occurring in the case of tissues in which the cell-sap is normally red during their fullest development. The brilliant scarlet of the fully expanded corollas of scarlet varieties of *Hibiscus rosa-sinensis* is replaced in the bud and in the fading condition by a dull red colour, which, especially in the latter case, is very much of the same character as that developed in the expanded corollas under the influence of chloroform. In the case of chlorophyll-containing tissues, and in those in which the cell-sap is of a blue colour when they are most highly developed, stimulation of protoplasmic activity appears to lead to relative alkalinity; and depression or abolition of protoplasmic activity to relative acidity; whilst, in the case of tissues containing red cell-sap, precisely the reverse is the case. The essential constituents of both red and blue colouring matters

appear to be the same, the tint being determined by the relative acidity or alkalinity of the medium. Hence blue flowers usually present a more or less purplish or reddish tinge in natural fading and when under the influence of chloroform, whilst red ones, on the contrary, lose their brilliancy and may even become almost colourless (like those of *Erythrina stricta*) under similar circumstances. The colour in *Erythrina stricta* is evidently related to intense acidity of the medium, for even perfectly neutral media reduce it very much, just as strong alkalis act on other red tissues, while the alcoholic extract demands an excessive addition of acid ere it reacquires a scarlet tint. Some blue flowers, such as those of the blue variety of *Clitoria Ternatea*, present an exception to the rule enunciated above, as they retain an intense blue colour during normal fading and exposure to chloroform, and they yield brilliant pure blue infusions and extracts on boiling and immersion in alcohol. This is not dependent on any peculiarity in the essential constituents of the colour, for the addition of acids to the blue extracts or infusions at once causes them to assume a beautiful red colour, but must apparently be due to the cell sap normally containing a relative excess of fixed alkaline constituents—an assumption which is favoured by the very feeble acidity which the freshly expressed sap presents. The extremely fugitive nature of the alkaline constituents in some other cases is most strikingly exemplified in cases where flowers of *Ipomœa hederacea* are killed by means of exposure to low temperatures, as the following experiment shows:—

Experiment XIII.—A fully expanded and normally coloured flower was enclosed in a metal box, and the latter was then buried in a mixture of pounded ice and salt, where it remained for an hour and a half. At the close of this period the flower remained fully expanded and retained it original colouring, but was frozen and rigid. On removal from the box immediate collapse occurred, and the colours of the normally blue and red areas at once changed, the former becoming violet and the latter ochreous. The white coloured portion at the base of the tube retained its colour somewhat longer, and then, like the red ones, became ochreous, the blue portions having meantime passed on from purple to dull red.

Immersion of flowers of the same species in boiling water is followed immediately by total collapse and similar changes in colour, but the results in this case are not so striking, as they are not so conclusively ascribable to mere cessation of protoplasmic activity as where they follow exposure to cold. The absence of collapse and the retention of the normal colour in the latter case, so long as the tissues remain frozen, must apparently be due to the cell sap being congealed so rapidly that no appreciable escape of liquid or discharge or decomposition of the fugitive alkaline or acid constituents present in it have time to occur. The process of rapid congelation not only arrests the manufacture of the products of protoplasmic activity on which the turgescence and colour of the tissues depend, but it for the time being retains those which are present in the sap at the moment at which congelation occurs. On the tissue thawing, an immediate loss of turgescence occurs, and this is accompanied by the escape or decomposition of the products of certain constituents of the cell sap to which its normal colour is due. It would be hard to find a more striking instance of the coincidence of loss of turgescence with alterations in the chemical constitution of cell sap.

It is only where the colours of the tissues depend on the presence of dissolved pigments, the tints of which are determined by the presence of fugitive acid or alkaline substances, that they serve as satisfactory indices to the occurrence of chemical changes

in the sap. In the case of blue *Clitoria* the tint is certainly related to relative alkalinity of the sap, but this alkalinity is in great part due to the presence of non-fugitive, fixed materials. In many yellow flowers, on the other hand, the persistence of the colour after death of the tissues depends on much of the colouring matter being insoluble in the sap. In the African marigold, for example, the greater bulk of the pigment of the corolla is not in solution, but is deposited in the form of resinous granules which are quite insoluble in water, and therefore any changes in the reaction of the cell-sap do not appreciably affect their colour. The fact, therefore, that in certain cases we do not find loss in turgescence in the tissues to be accompanied by any conspicuous change in their colour, cannot be taken as any evidence that chemical changes in the nature of the cell-sap have not occurred; whilst the constancy with which we encounter evidences of the presence of such changes, in cases where indices to their occurrence are present, strongly supports the belief in the normal coincidence of alterations in turgescence, which depend on fluctuations in functional activity of the protoplasts, and chemical changes in the cell-sap.

The chromatic change accompanying depression or abolition of function in vegetable tissues is not, of course, an absolute proof of coincident alterations in their osmotic properties, but merely of alterations in the composition of their cell-sap. It is, however, highly probable that the processes leading to the latter may affect the former also, and there are certain phenomena which to a certain extent appear to indicate that they actually do so; for in cases in which depression and abolition of functional activity is accompanied by very marked chromatic changes, we find the coincident loss in turgidity excessive, whilst in cases where chromatic changes are inconspicuous, the loss in turgidity is not nearly so great. For example, when the flowers of blue *Clitoria* are killed by continued exposure to the vapour of chloroform, hardly any change manifests itself in their colour, whilst in the case of flowers of scarlet *Hibiscus* under similar circumstances the change is very great. A corresponding difference occurs in relation to the coincident loss in turgidity, for, although there is a considerable loss in *Clitoria*, it is limited in degree as compared with that occurring in *Hibiscus*, in which the great change in colour is accompanied by absolute flaccidity of texture. The absence of conspicuous change in colour, and the limitation in loss of turgescence, in *Clitoria* are at all events both ascribable to the presence of certain stable constituents in the cell-sap which serve to maintain conditions in it subsequent to the death of the tissues which can only be maintained in *Hibiscus* as the result of the continued exercise of functional activity.

The experimental data which have been given above afford sufficient evidence that alterations in turgescence following exposure to influences of the most diverse nature, and which can hardly be supposed to produce any common effect on the nature of the protoplasts of the tissues beyond depressing and ultimately abolishing their functional activities, are accompanied by conspicuous alterations in the chemical constitution of the cell-sap. This in itself is sufficient to suggest that it is to the properties of the latter, and not to those of the protoplasts, that turgescence is immediately related; but we are not obliged to remain content with any ambiguous evidence, as it is not hard to find examples in which turgescence persists even in a very high degree quite apart from the presence of any living protoplasts in the tissue. The tissue of the mesocarp of a ripe orange is one of the most striking of these. Here we certainly have a highly turgid mass of tissue in which turgescence is maintained in spite of the absence of

any living protoplasm During the process of maturation, the protoplasts of the cells have been gradually expended with a proportionate accumulation of the products of their functional activity in the cell sap, and in the fully ripened tissue, if any living protoplasm persists, its amount must evidently be extremely small Whatever its amount be, however, it certainly is not the cause of the turgidity of the tissue, as we find the latter persisting under circumstances which involve the death of any living protoplasts which have been exposed to them When, for example, we expose portions of the mesocarp of an orange to the influence of the conditions which we have just seen to cause loss of turgescence where the latter is dependent on the presence of living protoplasts, we do not find any evidence in these portions of the occurrence of parallel change This is shown by the results of the following experiments —

Experiment XIV—A segment of the mesocarp of a ripe orange, weighing 10 58 grammes, was exposed in a chloroform chamber for twenty four hours At the close of this period it weighed 10 6 grammes and retained its turgidity unaltered

Experiment XV—A segment, weighing 9 52 grammes, was exposed in a chloro form-chamber for twenty four hours At the close of the experiment it weighed 9 53 grammes

Experiment XVI—A segment, weighing 13 5 grammes, was immersed for forty minutes in a 2 5 per cent alcoholic solution of corrosive sublimate On removal its weight had increased to 13 73 grammes It was now placed in a simple moist chamber, and on the following day was found apparently just as it had been at the beginning of the experiment, quite turgid, the surface dry, and the weight 13 5 grammes

Experiment XVII—A segment, weighing 20 44 grammes, was immersed in a 2 5 per cent solution of corrosive sublimate for twenty four hours At the close of that period it was excessively turgid, and when dried weighed 20 64 grammes It was now placed in a simple moist chamber Twenty four hours later it was quite turgid the surface dry, and the weight 19 87 grammes It was kept under observation for three days longer, and at the end of the experiment weighed 19 5 grammes

Experiment XVIII—A segment of the mesocarp of a ripe orange (*a*), weighing 13 08 grammes, and a leaf of *Kalanchoe* (*b*), weighing 17 24 grammes, were immersed for one minute in boiling water On removal (*a*) weighed 13 5 grammes and (*b*) only 15 65 Forty eight hours later, (*a*) weighed 12 54 grammes, whilst (*b*) was flaccid yellowish olive, and weighed only 14 6 grammes, the total loss in the former amounting to 4 1 per cent and in the latter to 15 3 per cent

One of the most striking examples of the maintenance of an extremely high degree of turgidity in cells, independent of the presence of any continuous stratum of living protoplasm, is that which is afforded by the fertile filaments of *Pilobolus crystallinus* The excessive turgescence in these, which ultimately leads to their rupture and the violent discharge of the sporangia, arises only after they have been almost entirely emptied of protoplasm by the onward progress of the latter and its accumulation within the sporangium, and certainly when no continuous stratum invests the interior of the cell wall It is certainly, therefore, independent of any anti filtrative property of protoplasm, and indeed is apparently independent of the action of any local protoplasm altogether, as we find it to be present in cases in which even the lower part of the stem immediately

above the great basal cell is apparently quite empty of all save fluid. At the same time it is clearly related to continued protoplasmic activity, although this is not carried on locally. This is shown very strikingly in cases where the mycelium and basal cells are subjected to the influence of osmic acid. If a mass of the cowdung on which a crop of fertile filaments in full turgescence is situated be moistened by a 2 per cent. solution of osmic acid, and set under a dissecting microscope, a very beautiful and interesting series of phenomena manifest themselves within the course of a minute or two. Under normal circumstances, of course, the turgescence in the fertile filaments is so excessive as to give rise to such a considerable excretion of fluid that they are studded throughout by beads of it. Under the influence of the osmic acid these beads may be seen rapidly to enlarge, and as they do so the filament gradually becomes flaccid and collapses. The very fact that this rapid and complete collapse should attend the action of osmic acid is in itself very strong evidence that the turgescence is independent of the presence of any continuous stratum of protoplasm, seeing that the fixative property of this re-agent for tissue elements seems to be due to its action in rendering the protoplasm relatively impermeable; and, when taken along with the histological evidence, it seems conclusively to indicate that we are here dealing with turgescence due to extrinsic agencies, due to the presence of materials which have not originated locally, but which, having been developed in connection with the functional activity of the mycelium and specially of the basal cells, have passed on into the interior of the fertile filaments. Further, it is evident that these materials must be of unstable nature, so that turgescence can only maintain itself against the factors making for filtration so long as a constant supply of them is being manufactured elsewhere and subsequently transferred to the cavities of the filaments.

Perhaps the most convincing proof of the indirect relation which turgescence bears to protoplasmic functional properties, and of its direct dependence on osmotic peculiarities in the cell-sap, is that which is afforded by the results of experiments in which, in the course of killing the protoplasts of the tissues, we secure the artificial addition of osmotic constituents to the sap. When we do so, we find in dealing with succulent tissues, such as those of *Kalanchoe*, in which an abolition of protoplasmic activity is normally accompanied by a very large discharge of fluid and loss in weight and turgescence, that death is not accompanied by any considerable diminution in weight or turgescence, and that the dead tissues may persist for prolonged periods in a highly turgid condition. The following experimental details illustrate very clearly the different effects produced on turgidity of tissue where death is determined with or without the addition of osmotic materials to the cell-sap:—

Experiment XIX.—Two leaves of *Kalanchoe*—one, *a*, weighing 28·22, the other, *b*, 27·54 grammes—were taken and set with the bases of the petioles immersed in water. The lower extremities of the petioles were then cut off subaqueously, so as to permit of free absorption, and leaf *a* set in a chloroform-chamber, and *b* in an ammoniacal one. Copious sweating set in in *a* within half an hour, and advanced so rapidly that the lobes had begun to collapse within an hour from the beginning of the experiment, the tissue at the same time beginning to acquire a yellowish tinge. In the case of *b*, a limited amount of exudation appeared very rapidly, and the tissue acquired an intense deep green tint, but no considerable loss of fluid occurred, and the leaf remained perfectly firm and showed no signs of collapse. The ammonia appeared to act more rapidly in causing

exudation than the chloroform, but the action appeared very soon to be arrested before sufficient loss had occurred to induce appreciable loss in turgidity, whilst, in the case of the chloroform, when exudation had once been established it advanced rapidly and steadily. On the following day the leaf *a* was of a pale yellowish olive colour and perfectly flaccid and collapsed, whilst *b* was deep dark green and quite firm and turgid. The loss of weight which had occurred in *a* was 7·75 grammes, or 27·4 per cent., and active exudation was still taking place. In the case of *b* the loss only amounted to 1·64, or 5·9 per cent., and there was no sign of any continued exudation. Subsequently to this *b* only was kept under observation, *being weighed at intervals and having a fresh petiolar* surface exposed each time that it was returned to the chamber. Twenty-four hours subsequently to the previously recorded observation, in place of showing any loss of weight, it showed a gain of 0·42, and a week after the initiation of the experiment the tissue remained highly turgid, and the total loss of weight for the entire period only amounted to 1·64 grammes, or 5·9 per cent. The weights at different periods are shown in the following table:—

Date	Weight in grammes	Total loss	Percentage loss
February 13th	27·54		
" 14th	25·90	1·64	5·9
" 15th	26·32	1·22	4·4
" 16th	26·31	1·23	4·4
" 17th	26·31	1·23	4·4
" 18th	26·32	1·22	4·4
" 20th	25·90	1·64	5·9

Up to the 16th the leaf remained continuously in the ammonia chamber, but it was then removed and kept in a simple moist chamber during the rest of the experiment. When removed it had a very strong ammoniacal odour, and for several days it continued to give off enough ammonia to endow the water in the water vessel of the moist chamber with a strong smell of it. Whilst in this chamber it discharged a considerable amount of fluid from the terminal lobe, which happened to be sloped rather abruptly downwards, the exudation beginning to appear soon after transfer from the ammonia chamber, and continuing steadily until the end of the experiment, in spite of the inappreciable loss in weight which accompanied it. The fact that an actual increase in weight manifested itself during the course of the second twenty-four hours of the experiment is remarkable, and is probably to be ascribed to a continued absorption of ammonia and increase in osmotic property of the cell-sap during that period partially making good the initial loss of natural osmotic property which had attended the death of the tissue. The artificial addition of ammonia to the cell-sap does not suffice to maintain the osmotic capacities of the latter at quite the normal level, but it prevents the great loss in osmotic property attending the cessation of functional activity from producing the effects which it naturally would give rise to. The loss in functional osmotic property appears to proceed more rapidly than the acquisition of artificial osmotic property, and hence an initial fall in turgescence below the level at which the artificial property, when fully developed, is able to maintain it.

Experiment XX.—A leaf of *Kalanchoe laciniata*, weighing 27·13 grammes, was set in a moist ammonia chamber with the base of the petiole, which had been subaqueously

divided, immersed in water. Twenty-four hours later it weighed 25·94 grammes, corresponding to a loss of 1·19c.c. of fluid, or 4·3 per cent. of total weight. The weights for the first six days of the experiment during which it was kept in the original chamber, having the petiole freshly subaqueously divided every day after weighment, were as follows:—

Date.	Weight in grammes.	Percentage loss in total weight.
March, 2nd	27·13	4·3
„ 3rd	25·94	4·3
„ 4th	25·96	4·3
„ 5th	26·16	3·5
„ 6th	26·21	3·3
„ 8th	26·21	3·3

After the first 24 hours, in spite of the fact that it daily discharged a large quantity of fluid, an actual increase in place of any further decrease in weight occurred up to a certain point, the tissue at the same time remaining excessively moist and turgid. On the 8th of March it was transferred to a simple moist chamber, and the petiole was no longer immersed in water. It remained in this for the next six days, during which the weights were as follows:—

Date.	Weight in grammes.	Percentage loss in total weight.
March, 9th	25·87	4·6
„ 10th	25·67	5·3
„ 11th	25·49	6·0
„ 12th	25·26	7·2
„ 13th	25·09	7·5
„ 14th	24·90	8·2

It was now once more set with the freshly divided extremity of the petiole in water, with the result that it again began to discharge water actively and at the same time gained considerably in weight, as shown below:—

Date.	Weight in grammes.	Percentage loss in total weight.
March, 15th	25·72	5·1
„ 16th	25·62	5·5
„ 17th	25·64	5·4
„ 18th	25·63	5·5

This experiment is specially instructive on several grounds. It affords a most perfect demonstration of the fact that, even in those cases in which the maintenance of turgidity is normally dependent on continued vitality of the protoplasts of the tissues, the relation between the two conditions is not a direct one determined by any structural peculiarities of the living protoplasm, but indirect and maintained through the intervention of the presence of certain osmotic properties in the cell-sap. The protoplasts of the tissues of this leaf had certainly been killed on the 2nd of March, and yet turgidity persisted in high degree sixteen days later, without there being any obstruction to the free passage of fluid through the tissues, as was clearly

shown by the continuous discharge which accompanied free supply of water A striking illustration is also afforded of the dependence of turgidity not only on intrinsic, but also on extrinsic conditions, not only on osmotic capacity of the cell sap, but on conditions of general loss and supply of water It cannot be supposed that any appreciable increase in osmotic property of the tissues occurred between the 14th and 15th March, and yet a very considerable rise in turgescence took place then, coincident with renewed free supply of water.

The contrast between the results in cases of this kind and those presenting themselves where death of the tissue is determined by means which do not intro duce permanent artificial osmotic properties into it, comes out very clearly on com paring the above figures with those furnished by an experiment on the results follow ing immersion in an alcoholic solution of corrosive sublimate —

Date		Weight	Loss	Percentage loss
December	21st	29 22		
„	22nd	26 44	2 78	9 5
„	23rd	24 68	4 54	15 5
„	24th	22 92	6 30	21 5
	25th	21 82	7 40	24 2
„	27th	21 03	8 19	28 0
„	30th	20 50	8 72	29 8

Even here, however, the initial loss of fluid and turgescence is not so great as in cases where the functional activity of the tissue is abolished by means of extremes of temperature, vapour of chloroform, or other conditions in which no appreciable addition of extraneous materials to the cell sap is involved The peculiarity of the phenomenon of artificial maintenance of turgescence by means of ammonia lies in its persistent character In cases of poisoning by alcoholic vapour under conditions of free water supply, the loss of fluid and of turgescence during the first twenty four hours is relatively limited, and may even fall as low as it is where ammonia is the toxic agent, but there is no permanent arrest established, and the loss, although retarded in the outset, goes on steadily progressing Exposure to an atmosphere of ammonia is followed almost immediately by a certain amount of discharge of fluid and con spicuous change of colour in the tissues, the abolition of functional activity being apparently much more rapid than where chloroform is employed, but, because the ammonia is readily absorbed by the cell sap and imparts certain properties to it, the loss of turgescence connected with the cessation of the normal manufacture of osmotic materials is very soon arrested, whilst chloroform (acting purely in arresting functional activity) does nothing to prevent the elastic recoil of the cell walls from exert ing its full effect

The effects of ammonia in artificially maintaining turgescence are specially conspicuous and measurable in dealing with succulent tissues such as those of *Kalanchoe*, but they also come out very clearly in many other cases, such as those of the two following experiments —

Experiment XXI—Two fully expanded flowers of scarlet *Hibiscus* were taken and the extremities of their stalks were freshly divided under the water of the vessels in

which they were set. One of them, *a*, was now placed in an ammonia-chamber, and the other, *b*, in a chloroform one. The petals of *a* immediately began to show purplish black spotting, which rapidly extended over their entire surface. The colour next gradually assumed a greenish tint and ultimately became of a fine warm ochre. Whilst these changes were occurring there were no signs of loss of turgescence, and it was not until some hours after their full completion that a little exudation and a trace of collapse manifested themselves. In the case of *b* the action of the abnormal medium did not manifest itself for some time; but, when once initiated, alteration in colour and loss of turgescence ran hand in hand, and after the close of a few hours the colour was of a dull maroon red and the tissues of the flower were completely flaccid and collapsed. Twenty-four hours after the initiation of the experiment, *a* was slightly collapsed, but after this it remained apparently unaltered for some days.

Experiment XXII.—Two flowers of scarlet *Hibiscus* were taken, and one, *a*, suspended free, apex downwards, in an ammonia-chamber, whilst the other, *b*, was similarly hung in a chloroform-chamber. In the case of *a*, discolouration, in the form of black spotting of the petals, made its appearance at once, and within an hour the red had entirely gone, save in a few isolated patches, and the rest of the tissue was deep purplish-black, passing into deep greenish and ochre at the margins. There was, however, no indication of any tendency to collapse. In *b* discolouration was developed much more slowly; but at the close of an hour the original vivid scarlet had been replaced by a deep maroon, and the petals, which had originally been highly reflexed, were drooping downwards and rapidly collapsing. The first traces of collapse in *a* did not appear until three hours after the beginning of the experiment, and even then the petals remained highly reflexed. On the following day the petals of *a* were drooped, but still widely divergent and firm in texture (plate III. fig. 3); whilst those in *b* hung vertically downwards and were perfectly flaccid (plate III. fig. 4). Twenty-four hours later the petals of *a* were slightly less divergent than they had been, but were still so divergent as to allow the stigmas to be visible beyond them in profile. Both flowers were now removed from the chambers and hung in the open laboratory, where they remained for days apparently unaltered, *b* being fully collapsed and *a* retaining a considerable amount of turgidity.

Experiment XXIII.—Two flowers of scarlet *Hibiscus* were, as in the previous case, placed respectively in ammonia and chloroform-chambers. They were not, however, suspended, but were set with the freshly, subaqueously divided extremities of their stalks immersed in water. As in the previous experiment, the flower in the ammonia chamber began to show black spotting immediately, and rapidly passed on through stages of deep purplish black and deep greenish to a uniform warm ochre without showing any signs of collapse; whilst that in the chloroform-chamber took some time to show any signs of change in colour, but when it once had begun to discolour, began also to collapse rapidly. On the following morning a slight amount of collapse only was evident in *a*, whilst *b* was completely collapsed, flaccid, and soaked. The ammonia-chamber was allowed to stand unopened for a week, and during that period *a* remained almost in the same condition as it was in after twenty-four hours' exposure.

From the results obtained in the first of these experiments it is evident that the retention of turgescence in such cases is not wholly due to the presence of free

ammonia in the tissues but that combinations must be formed within the cell sap which render it more or less permanently hygroscopic The flower *a* did not undergo complete collapse on removal from the ammonia chamber, but remained partially turgid even after prolonged exposure in the open air There can, therefore, be no doubt that turgescence is mainly, if not solely, due to the osmotic properties of the cell sap, and that losses in turgescence are due to diminished osmotic capacity in the latter, and not to any increased filtrative properties in the protoplasm It is not, however, quite clear that structural alterations in the protoplasm may not act in the contrary direction, in the way of retarding losses in turgescence by presenting an abnormal resistance to the elastic recoil of the cell walls When we consider the phenomena presenting themselves in connection with death of tissues under the influence of the vapour of osmic acid, there are many points suggesting that the abnormal slowness with which loss of turgescence advances is due to such a causation This is shown by the data furnished by the next two experiments

Experiment XXIV—A leaf of *Kalanchoe*, weighing 8 38 grammes, was enclosed in a moist chamber containing a vessel of 2 per cent solution of osmic acid Visible blackening of the surface became apparent within the course of half an hour, but the first drop of exudation did not appear until two hours after exposure, and an hour later only a certain number of scattered drops of black fluid had been excreted On the following day the leaf was coal black and bore numerous large inky drops of fluid, but the texture remained quite firm and the weight was still 7 9 grammes It was now placed in a simple moist chamber, where it remained for the next twelve days The successive losses in weight which occurred during the entire course of the experiment are recorded below —

Date	Weight	Successive losses	Total percentage loss
January 26th	8 38		
„ 27th	7 90	0 48	5 7
28th	7 78	0 12	7 1
29th	7 64	0 14	8 6
„ 30th	7 57	0 07	9 6
31st	7 49	0 06	10 6
February 2nd	7 30	0 19	12 8
„ 3rd	7 20	0 10	14 0
4th	7 05	0 15	15 6
„ 5th	6 91	0 14	17 5
6th	6 84	0 07	18 3
„ 8th	6 60	0 24	21 2
„ 9th	6 52	0 08	22 1

Here we have evidence of retarded loss in turgescence, but the losses continued to progress steadily, and there was no evidence of the absolute arrest of loss manifesting itself in the case where death was caused by exposure to ammonia—*vide* experiment XIX The phenomenon appears rather to be the parallel of that presenting itself in cases where the tissues are frozen, only that in this case the obstruction to the escape of volatile constituents and water from the tissues is a permanent one and does not, like that established by cold, disappear on removal of the tissues from the conditions under

which it originated. In cases of exposure to an atmosphere of ammonia there is no evidence of any initial obstruction to the escape of fluid; on the contrary, exudation manifests itself with special rapidity, and it is only after some time that loss of turgesceenc ceases to occur and a condition of equilibrium is established between the osmotic capacities of the tissues and the elastic recoil of the cell-walls; but, when equilibrium has been arrived at, it is stable. In the case of exposure to an atmosphere of osmic fumes, on the other hand, we have from the outset very distinct evidence of the action of a factor obstructive to the normal loss in turgescence attending death. Exudation appears exceptionally late and advances very slowly; but, once established, it advances evenly and continuously, and there is no tendency to any establishment of a stable equilibrium until the elastic recoil of the cell-walls has been fully satisfied. We have here evidence showing that alterations in the protoplasm may retard the progress of the effects following loss in osmotic property in the cell-sap, but none to show that any mere alterations in the protoplasm will suffice to give rise to loss in turgescence so long as the osmotic properties of the cell-sap remain unaltered.

Experiment XXV.—A leaf of *Kalanchoe*, weighing 27·7 grammes, was set in an osmic acid-chamber on the 15th of March, the base of the petiole being immersed in water and having been freshly divided subaqueously. On the following day it was entirely blackened and had exuded numerous large drops of inky fluid along the margin of the lobes, but the weight, in place of being decreased, was slightly increased, probably due to the addition of constituents from the osmic acid more than counterbalancing the loss in weight occasioned by the exudation. It was now set in a simple moist chamber, the petiole not being in water. It remained thus for the succeeding five days. The weights from the beginning of the experiment up to the close of this period are shown below :—

Date.		Weight.	
March 15th	... ...	27·7	
„ 16th	... ...	27·72	= + 0·02
„ 17th	... ...	27·13	= — 0·59
„ 18th	... ...	26·74	= — 0·39
„ 19th	... ...	26·30	= — 0·44
„ 20th	... ...	25·05	= — 1·25
„ 21st	... ...	24·40	= — 0·65

The percentage loss on total weight was now 11·9, or somewhat greater than that which the ammoniated leaf of experiment XX had sustained at the close of the period during which it had been kept apart from water in a simple moist chamber. The petiole was now once more set in water and subaqueously divided. The leaf was kept thus for three more days, being daily weighed and anew set in water with a freshly subaqueously exposed petiolar surface. Weighments for the period were as follows:—

Date.		Weight.	
March 22nd	... ...	23·62	= — 0·78
„ 23rd	... ...	23·32	= — 0·30
„ 24th	... ...	23·09	= — 0·23

The results of this experiment very clearly show that the action of osmic acid in preventing a loss of turgescence on the death of the tissues is quite distinct from that of ammonia The loss of turgescence is greatly retarded, and may even initially be obscured altogether, owing to the addition of new weighty constituents of the tissues, but there is no absolute arrest of it after a certain point as there is in the case of ammoniated tissues when freely supplied with water In the case of the ammoniated tissues the evidence points unequivocally to an artificial maintenance of osmotic property, in that of those acted on by the osmic acid to the establishment of an obstruction to filtration impeding the action of the elastic recoil of the cell walls in effecting the discharge of fluid from the interior of the cell cavities The total loss of weight in the case of the ammoniated leaf during a period of twenty three days amounted only to 1 47 grammes, or 5 4 per cent, and of this 1 19 or 4 3 per cent occurred within the first twenty four hours, the loss in the leaf exposed to osmic vapour during a period of nine days amounted to 4 61 grammes or 16 6 per cent, and was steadily progressive and unaffected by the freest supply of water to the tissues, whereas in the ammoniated leaf immediate recovery of weight followed renewed supply of water

If the filtrative resistance of the protoplasts of a tissue be artificially elevated, as it appears to be under the influence of osmic acid, the loss in turgescence normally accompanying loss in osmotic capacity in the cell sap will be retarded because the elastic recoil of the cell-walls now encounters an abnormal opposition, and if a mass of turgid tissue be exposed to sufficient external pressure, a diminution in its turgescence will necessarily take place apart from any loss of osmotic capacity, because filtration will now no longer be dependent merely on the elastic recoil of the cell walls, but on this, aided by external pressure But whilst this is the case—whilst the actual degree of turgescence present in any given tissue is liable to be affected by its filtrative as well as its osmotic condition—there is no evidence to show that under normal circumstances, any mere alterations in the inherent filtrative properties of the protoplasm of a tissue, apart from alterations in the osmotic properties of its cell sap, are efficient to give rise to appreciable changes in its turgidity, and the belief that they do act in such a fashion is simply based on the arbitrary assumption that the exercise of contractile function—that mere change of form in the living elements of a tissue—is capable of giving rise to alterations in its turgescence, which, of course, necessitates the second *assumption that the change in form is accompanied by a change in filtrative resistance* The protoplasm in ammoniated leaves of *Kalanchoe* has probably lost considerably in filtrative resistance, and yet the tissues retain a high degree of turgescence, whilst, in cases where the leaves are exposed to the influence of the vapour of chloroform, there is no reason to suppose that there is any depression of filtrative resistance, and yet total loss of turgescence occurs

The belief that the essential determinant of turgescence lies in certain physical peculiarities of protoplasm, and not in the properties of its products, and that any losses in turgescence which are related to functional causes are due to increased filtrative power in the protoplasts of a tissue, has no doubt arisen because of the striking fluctuations in turgescence accompanying depression or cessation of protoplasmic activity in cases where the osmotic products of the latter, on the presence of which turgescence depends are very unstable, and must therefore be constantly renewed in order to the maintenance of turgidity In the vast majority of cases, the protoplasmic products on which the colour and turgescence of the tissues depend are very unstable, and hence any considerable

fluctuations in the rate of their manufacture are at once followed by conspicuous alterations in tint and texture. In a certain number of cases, however, they are stable, and here an entire cessation of protoplasmic activity may occur without giving rise to any appreciable results. In the first instance, death gives rise to immediate alterations in colour and turgescence; in the latter, it produces no appreciable effect. Turgescence is normally solely dependent on certain properties of the cell-sap; and, so long as these are retained, it is a matter of indifference whether living protoplasm be present or not, or what changes in form it may undergo. In so far as intrinsic conditions are concerned, it is loss of osmotic properties in the cell-sap, and not any direct alteration in the structure of the protoplasm, that gives rise to loss of turgescence: but, in dealing with any experiments on tissues in which the maintenance of turgescence is normally related to continued vitality, we have carefully to bear in mind that certain extrinsic conditions may come in to modify the nature of the results accompanying a cessation of functional activity.

In cases where the cessation of functional manufacture of osmotic products is accompanied by the introduction of extrinsic products (as in experiments where the leaves of *Kalanchoe* or the flowers of *Hibiscus* are exposed to an atmosphere of ammonia), the loss of turgescence attending the death of the tissues is reduced to a minimum; whilst, in cases where no such modifying influence is present, the amount of loss will be determined solely by the extent to which any stable osmotic materials of intrinsic origin are present. In all such experiments we have to consider the influence of the conditions to which the tissues are exposed in producing the following effects:—

1st—Cessation of functional activity.
2nd—Addition of extraneous osmotic constituents to the cell-sap.
3rd—Disturbances in the relations of supply and evaporative loss of fluid.
4th—Alterations in the filtrative power of the protoplasm, and possibly of the cell-walls.

In cases where leaves such as those of *Kalanchoe*, or flowers such as those of *Hibiscus rosa-sinensis*, are exposed to an atmosphere of ammonia in a moist chamber, and with the bases of their stalks subaqueously divided and immersed in water, we find turgescence remaining almost unaffected by the death of the tissues, because of the addition of extraneous osmotic materials to the cell-sap co-existing with free supply and abolished evaporative loss of fluid. Where similar tissues are exposed to an atmosphere of chloroform under otherwise like conditions, an abolition of turgescence follows the cessation of functional activity, because the freest supply and abolished evaporative loss of water will not make up for the loss of osmotic properties in the cell-sap in resisting the elastic recoil of the cell-walls. Where, as in experiment XXI of chapter II, the same tissues are exposed to an atmosphere of ammonia, without special provisions for securing supply and abolishing evaporative loss of water, a very considerable loss of turgescence takes place in spite of the addition of extraneous osmotic materials to the cell-sap; and finally, where they are exposed to the action of osmic vapour, the loss in turgescence associated with abolition of functional activity is retarded, apparently owing to the introduction of obstacles to filtration. Such obstacles do not, however, arrest the loss of turgescence; they merely retard it, whereas the introduction of extrinsic osmotic materials bring it to a standstill whenever their capacities come to equilibrate those of the elastic recoil of the cell-walls. The effect of loss of osmotic property in the cell-sap may be retarded by obstacles to

filtration, but we have no positive evidence to show that any loss of turgescence ever arises owing to the development of special filtrative facilities in the protoplasm apart from alterations in osmotic property of the cell sap The elastic recoil of the cell walls is the essential factor in maintaining the pressure which makes for filtration and is constantly struggling with the osmotic capacities of the cell sap When a condition of equilibrium has been established between these opposed agencies, it will remain stable so long as they remain unaltered, but will be disturbed by anything affecting their mutual relations Any rise in osmotic capacity of the sap will thus at once tend to increase turgescence, and any rise in external pressure will tend to diminish it, and it is only where fluctuations of equal value occur in both simultaneously* that turgescence will remain unaltered

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CHAPTER IV

The extrinsic agents affecting turgescence

In the previous chapter we have seen reason to believe that turgescence is essentially dependent on certain osmotic properties in the cell sap which cause the cell cavities to include more fluid than their passive structural peculiarities will account for We have now to consider the influence of certain extrinsic factors in affecting the actual degree of turgescence present at any particular time The functional activities of the protoplasts of the tissues provide that the cell sap shall have certain osmotic capacities but the degree of turgescence at any time must be affected by the extent to which the latter are able to satisfy themselves Protoplasmic activity secures the presence of osmotic products but external conditions must determine the extent to which these will be able to give rise to turgescence The nature and quantity of osmotic materials in a mass of tissue may remain unaltered, and yet, in spite of this its degree of turgescence may vary greatly, owing to variations in the amount of water available for them to act upon The total mass of water contained within any terrestrial plant is subject to constant variations which are due to fluctuations in root supply and evaporative loss and where the former of these is defective or the latter excessive the highest degree of protoplasmic stimulation and activity will be unable to maintain the turgescence of the tissues to its normal extent Solar stimulation certainly tends to establish the maximum of turgescence in chlorophyll containing tissues where sufficient water is available to allow them to satisfy their osmotic properties, but the strongest solar stimulation will not suffice to prevent loss of turgescence under conditions of defective supply or excessive loss of water Every one, and specially every one who has lived in the tropics, must be familiar with the phenomena of temporary wilting in certain common leaves and the assumption of the nocturnal position by nyctitropic ones which so constantly manifests itself in the early part of the afternoon during hot dry weather The two phenomena have been by some observers regarded as the results of two distinct causes, wilting of common leaves being allowed to be the result of deficient water supply,* whilst the movement in nyctitropic leaves is ascribed to the direct action of excessive solar stimulation,† but the following experimental data clearly

* Sachs Vorlesung XIV s 274
† Sachs Vorlesung XXXVI s. 767

demonstrate that, in both alike, the essential determinant lies in the relation between supply and loss of water:—

Experiment I.—At 2-30 P.M. of a bright afternoon in November, the leaflets of four plants of *Cassia alata*, growing in rather small pots, were all in almost complete nocturnal position, whilst those of a plant of the same species, situated side by side with them and under precisely the same conditions in regard to insolation, but growing in the ground, were in a state of full expansion. One of the pots was flooded with water, and an hour later the leaves of the plant in it were almost fully expanded, whilst those of the other pot-plants remained as before in the nocturnal position. At the same time the leaves of an *Eranthemum* growing beside the *Cassias* were very considerably wilted. Here there were indices to the occurrence of general loss of turgescence in the *Eranthemum* leaves, and of local loss of turgescence in certain masses of tissue in the leaves of the *Cassias* in pots, determined, in the latter at all events, simply by defective root-supply in relation to transpiratory loss.

Experiment II.—At 1-30 P.M. on another day the leaves of two pot-plants of *Cassia alata* had their pinnæ in almost fully developed nocturnal position. One pot was flooded with water, and at 2-50 P.M. the pinnæ of the plant in it were almost fully expanded, whilst those of the other remained as before.

Experiment III.—Two pot-plants of *Cassia alata* were set side by side on a flat masonry roof, so as to be fully exposed to the sun all day. At 1-20 P.M. of December 10th, one of them had its leaflets in the nocturnal position and the other its leaflets nearly in the same state. The pot containing the former was flooded with water, and three hours later the plant in it was fully expanded, whilst the other remained as before. The following day was a cool, dry one, with only feeble sunshine, owing to the general clouding of the sky; but in spite of this both plants were in partial nocturnal position at 1-30 P.M., the development of the nocturnal position being much more advanced in the plant in the pot which had not been flooded on the previous day than in the plant in the other. The former plant was now flooded. Twenty-four hours later its leaflets showed only a very slight tendency towards the assumption of the nocturnal position, whilst those of the other plant had to a great extent assumed it. The pot containing the latter plant was flooded, and at 4-30 the leaflets were found fully expanded, whilst those of the other plant remained as before in the initial stages of the nocturnal position.

It would be easy to multiply the record of experiments of this nature indefinitely, but, as the results were of a uniform nature, it would be superfluous to do so. Other nyctitropic leaves just as clearly show the influence which is exerted on turgescence by variations in the relations between root-supply and transpiratory loss. In warm, relatively dry weather, and under like exposure to sunshine, the leaves of pot-plants of *Pithecolobium saman* will be found to be in the fully developed nocturnal position, whilst those of plants rooted in the ground are in the fullest expansion. So again with the leaves of *Cassia sumatrana*. Two plants growing side by side and equally exposed to the sunshine, but one rooted in the ground and the other in the crevices in a wall, day after day in the afternoon during warm dry weather will respectively have their leaflets in full expansion and in the nocturnal position. In the above instances the most influential factor in giving rise to diminished turgescence under otherwise favourable circumstances was

insufficient root supply of water, but, of course, excessive transpiratory loss will produce similar effects, as the following experiment shows —

Experiment IV—Two leaves of *Kalanchoe laciniata*, each weighing exactly 10.38 grammes, were taken One of them (*a*) was placed in a simple sealed chamber, and the other (*b*) in one including capsules containing sulphuric acid and chloride of calcium The chambers were placed side by side in front of a window, so as to secure their equal exposure to light. Twenty four hours later, (*a*) remained quite plump and rigid and weighed 10.26 grammes, whilst (*b*) was flaccid throughout, slightly browned at some points on the margin, and weighed only 8.35 grammes Both leaves were now removed and planted with the bases of their petioles in moist earth, and here (*b*) shortly regained its turgidity save in the browned areas Here the influence of root supply was eliminated, as neither leaf had any source of supply whatever, and the excess of loss in weight shown by (*b*) as compared with (*a*) is thus to be credited solely to the action of excessive transpiratory loss The loss in weight in (*a*) amounted to 0.12 and may be taken to indicate the quantity of water required to saturate the air of the chamber together with any expended in the course of assimilatory processes This leaves a loss of 1.91 in (*b*), ascribable to excess of transpiratory loss determined by the aridity of the air of the chamber

It is the want of equilibrium between supply and loss that is the essential factor in determining the result, not any absolute amount of either The root supply during the course of the night must, as the soil cools, tend to diminish, and yet it secures the renewed turgidity of tissues which have wilted during the day, because it no longer has to contend with transpiratory loss Once the dew point has been arrived at, transpiratory loss comes to an end, and hence the continued supply, although not so great as during the day, is able to restore turgescence in spite of the diminished manufacture of osmotic products incident on absence of solar stimulation of the protoplasm That it is the cessation of transpiration, and not any other nocturnal condition, which is the efficient cause, is indicated by the fact that, on cloudy and dewless nights, recovery does not occur, but that, apart from increased water supply, the wilting is carried on continually into the next day The same thing is, as we shall see when we come to consider nyctitropic phenomena, very clearly indicated also by the fact that the nocturnal condition in tissues exhibiting these attains its maximum in the early part of the night, and then goes on gradually reverting, up to a certain point, towards the diurnal one

In endeavouring to account for any particular fluctuations in turgescence and for the effects following these, we have to consider not merely the conditions of protoplasmic activity regulating the manufacture of osmotic products, but also extrinsic conditions affecting general supply and loss of fluid The fullest stimulation of the protoplasm may be present (as in hot dry afternoons) coincidently with very imperfect turgescence, owing to deficient supply and excessive transpiratory loss of fluid, on the other hand, a high degree of turgescence may accompany defective stimulation, as it does during the latter part of dewy nights, because of the coincident continued supply and abolished loss of water The maximum of turgescence in tissues in which turgidity is dependent on continued vitality is only reached where they are exposed to coincident maximum stimulation of their protoplasts, to abundant supply and to abolished loss of water, but all minor degrees may be present where these various factors are otherwise combined In any ordinary plant under normal circumstances ceaseless insensible fluctuations in turgescence

must be taking place in connection with the varying degree in which the different factors are associated with one another. Every rise in protoplasmic stimulation, so far as it affects the manufacture of osmotic products; every rise in root-supply; and every fall in transpiratory loss, must make for increased turgescence: whilst every fall in protoplasmic stimulation or root-supply, and every rise in transpiratory loss, must tell in the opposite direction. In the vast majority of cases, however, no readily appreciable results ensue; and it is only where the fluctuations are considerable, and where the tissues present certain peculiarities of structure and arrangement, that we have conspicuous indices to their occurrence under normal circumstances.

CHAPTER V.

The effects produced by fluctuations in turgescence.

Fluctuations in the turgescence of masses of vegetable tissue may manifest themselves in the form of more or less conspicuous changes in bulk, consistence, colour, or position. Changes of the first kind present themselves very conspicuously in cases of artificial plasmolysis in linear series of cells. In these a general diminution in bulk is all that at first presents itself to observation; and it is not until this has advanced to a certain point, until the elastic recoil of the cell walls has been satisfied; or, in other words, until turgescence of the cells has ceased to exist, that detachment of the protoplasts occurs. Changes in consistence associated with fluctuations in turgescence cannot be better illustrated than by the temporary drooping and wilting which affects so many leaves during the course of hot, dry days, and which is recovered from when nocturnal conditions put a stop to transpiratory loss. Conspicuous changes of colour are comparatively rare and exceptional phenomena, but some very striking instances of their occurrence may be found. Among these is that which presents itself in connection with *Selaginella serpens.*

Here the fronds, which under normal conditions are of a brilliant green during the day, become towards, and for some time after, sunset of a chalky whitish colour. This tint persists for some time and then gradually fades off, so that by midnight it has been apparently completely replaced by the diurnal one. The cause of these changes in colour can be readily determined by means of immersing portions of the fronds, whilst in the various states of coloration, in 2 per cent. solutions of osmic acid for a minute or two, and then making microscopical preparations from them. This treatment, as Ludwig Klein was the first to point out, not only fixes the protoplasts of the tissue in the form which they had when the specimen was taken, but also acts on the chromatophores in such a fashion as to cause them to retain their normal chlorophyll content and colour, even when the specimen is subsequently exposed to the action of alcohol and mounted in balsam, the result being that permanent preparations corresponding to the various changes in colour of the fronds can be obtained.

Before going on to describe the phenomena presented by any such series of preparations, it may be well to furnish certain details regarding the structure of the fronds. The greater part of their substance is composed of two strata of epidermis,

differing, however, from common epidermal tissues, inasmuch as all the constituent cells, with the exception of those of the marginal row bounding the frond and connected with both strata, are abundantly provided with chlorophyll, the cells of the superior stratum especially containing a variable number of relatively large chromatophores (plate I fig 6) The superior epidermis over the greater part of the frond consists of short polygonal cells, with wavy margins, and with numerous narrow pits or actual slits on the external or upper face of their walls (plate I fig 3) Towards the margins of the frond, the cells become somewhat more elongated, and the outer ones are in direct contact with the common marginal row, to which the external part of the inferior epidermis is also attached The marginal cells are, as before said, devoid of chlorophyll and are of a narrow, elongated figure, some being prolonged anteriorly into projecting points which give the frond a serrated contour (plate I fig 1) Their walls are greatly thickened and highly cuticularised, especially externally, and the projecting points are almost completely filled up so as to form solid spines

The inferior epidermis, except immediately over the midrib, is composed of elongated cells with strong walls and containing only a comparatively small quantity of chlorophyll (plate I figs 1, 2) A few stomata are present along the middle line of the superior epidermis, and a good many occur generally diffused over the inferior one The inferior epidermis and the highly thickened rim form a sort of rigid frame on which the superior epidermis is highly stretched in such a fashion that, even were its cell walls extensile and elastic, any considerable alteration in the capacity of the cell cavities is rendered impossible under ordinary circumstances Between the two epidermal strata there is a thin layer of very open tissue, which is somewhat thickened along the middle line around the single vascular bundle, but which thins out and disappears around the edges and distal extremities of the leaflets Each leaflet thus consists of a comparatively rigid inferior stratum, a very resistent margin, a superior stratum rich in chlorophyll and consisting of cells the walls of which are pitted towards the free surface, and a limited amount of loose intermediate tissue including a vascular bundle

The processes which determine the conspicuous changes in the colour of the frond take place in connection with the cells of the superior epidermis When we examine a series of preparations of this derived from fronds in maximal conditions of greenness and whiteness it becomes at once evident that the protoplasmic constituents of the cells are in very different states in the two cases In the bright green diurnal condition (plate I figs 4, 6), the protoplasts entirely fill the cell cavities and the separate chromatophores which they contain are more or less distinctly recognisable, whilst, in the maximal white state (plate I figs 5, 7, 8), the protoplasm is shrunken and contracted away from the cell walls, and the chromatophores are so closely packed together as to form a spherical mass in which the individual elements are irrecognisable, and which in many cases is the only visible representative of the protoplasmic content of the cell In other cases a narrow, irregular fringe of colourless, granular protoplasm, containing a nucleus, may be detected around more or less of the periphery of the chromatophoric sphere Between the outer margin of the protoplasm and the cell wall a wide space intervenes, which in the natural state of the tissue appears to be occupied by air, and it is to the presence of this intracellular air that the peculiar silvery or almost chalky whiteness of the fronds is due If, finally, we examine fronds in the green state which they assume during the latter part of the night (plate I fig 9), we find the

protoplasts in an intermediate condition, not nearly so highly contracted as they were when the plant was in the white condition, but at the same time not so turgid as in the diurnal green state, so that they do not fully occupy the cell-cavities and still leave narrow peripheral spaces between their outer surfaces and the interior surfaces of the cell-walls.

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simplest form, it is advisable to study it somewhat closely ere proceeding to the consideration of cases in which the movements are no longer determined by the mutual relations of individual cells, but by those of complicated masses of tissue. As every one is aware, the opening and closure of the stomatic orifices are due to the fact that, under certain conditions of illumination, root-supply, and transpiratory loss of water, the guard-cells become so turgid that they are able to determine a certain amount of displacement of the surrounding epidermal elements; and that, in the absence of these conditions, they lose turgidity to a greater or less degree, and, being no longer able to withstand the recoil of the neighbouring tissue, they allow it to approximate their inner surfaces and more or less completely to close the interspace between them. This, it is evident, implies that under favourable conditions the guard-cells become more turgescent and, for the time being, stronger than the other epidermal elements; for did they not do so displacement of the latter would be impossible. We have then in the first place to ascertain what are the distinctive features in the guard-cells as compared with the other epidermal elements, which are associated with this capacity for temporary increase in strength. And when we have done so we find them to be the following :—*1st*, they are younger than their neighbours; *2nd*, they are richer in protoplasm; *3rd*, they are conspicuous as containing a relative abundance of chlorophyll and starch; *4th*, they are, as Kienitz-Gerloff has shown,* distinguished by the fact that there is no continuity between their protoplasm and that of neighbouring cells. The three first of these characters are characteristic of the active elements in nyctitropic tissues generally; but the fourth is naturally absent in cases where movements are determined, not by alterations in the turgescence of isolated cells, but of masses of tissue. In the case of the guard-cells it is necessary that conditions providing for the excessive turgidity of individual cells should be provided, and accordingly we find the cell-cavities closed and the protoplasts isolated; but in the case of masses of active tissue there would, of course, be no advantage attained by the isolation of the individual units entering into their constitution.

That the guard-cells belong to a younger generation than the surrounding common epidermal cells is a well-recognised fact. In the first edition of the English version of Sach's "Text-book of Botany" we find it stated that "as the stomata do not arise until rather late, that is, during or after the expansion of the internodes and leaves, their arrangement is partly dependent on the originally elongated form of the epidermis cells," and that "the origin of the stomata is always the result of the formation of a mother-cell, first of all by division of a young epidermis cell, which is sometimes preceded by several preparatory divisions in it or in adjoining epidermis cells; and this mother-cell becomes more and more rounded off, and the guard-cells are formed from it by division."†

It is unnecessary to quote any special authority for the fact of the special abundance of protoplasm, and particularly of chlorophyll and starch, in the guard-cells as compared with other epidermal elements, as it is one which is evident to the most casual observation.

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* Die Protoplasmaverbindungen zwischen benachbarten Gewebe-elementen der Pflanze. F. KIENITZ-GERLOFF Bot. Zeit. 1891.

† A Text-book of Botany; Sachs. Bennett and Dyer, 1st ed., pp. 76, 87.

In the guard cells we have to deal not merely with younger elements, and therefore with elements which are for a time structurally weaker than the surrounding epidermal cells, but with elements which in certain areas remain permanently weak, owing to the characters of their walls, which, as is well known, remain permanently thin, extensile, and elastic on their lateral faces. They are not, however, merely structurally weaker than their neighbours, but they are also physiologically stronger on account of their relative excess of protoplasm, and specially of chlorophyll which, under the influence of sunlight, determines an excess of assimilatory activity and with this an excess of turgescence, due to the rise in osmotic capacity which the products of assimilatory activity determine in the cell sap, and which attains a specially high degree of development in consequence of the complete closure and isolation of the cell cavities. An equal rise in turgescence does not occur in the common epidermal cells, owing to their poorer protoplasmic content and deficiency in chromatophores, and hence under the influence of sunlight, the guard cells become for the time being relatively stronger than their neighbours, and are able to determine a certain amount of displacement of them. When assimilatory activity is no longer stimulated, the manufacture of osmotic products falls, and with this the turgescence of the guard cells ceases to be excessive and the elastic recoil of their own walls and of the surrounding displaced cells causes the tissue to resume the position proper to its passive condition as determined by the structural strength and arrangement of its constituent elements. The common epidermal cells are structurally stronger but functionally weaker than the guard cells, and hence are relatively weaker during periods when the tissue is exposed to sunlight than they are when it is in darkness. The guard cells, on the other hand, are structurally weaker but functionally stronger than their neighbours, and consequently attain their maximum relative strength during periods of insolation. The position of the cells during darkness represents the outcome of the structural features of the tissue along with the degree of turgescence persisting apart from photic stimulation of its protoplasts. The incidence of sunlight determines a greater rise in turgescence in the guard cells than in the surrounding elements, and consequently makes them relatively stronger than the latter are, and in doing so enables them to cause a certain amount of displacement of these. The removal of solar stimulation, on the other hand, gives rise to a general loss in turgescence, but, the loss in *the guard cells being greater than that in the common epidermal cells, the latter* now become the stronger and return to the position which they occupy apart from the action of the stimulus. The opening and closure of the stomatic orifices are, therefore, the results of the structural and physiological differences existing between the guard cells and the other epidermal elements, the relative structural weakness of the former determining closure in the absence of light, and the relative functional weakness of the common cells securing that opening shall occur on the incidence of solar stimulation.

It is clear that these movements, which are really nyctitropic when due to the presence or absence of light, may arise independently of any variation in conditions of illumination, so long as the variations in turgescence, which are their immediate causes, are present. As we have already seen the actual degree of turgescence in any tissue or tissue element at any given time depends not merely on the osmotic capacities of the cell sap, but on the amount of water available to satisfy these. Accordingly we find that, even under conditions of maximum solar stimulation, the stomatic orifices are more

or less closed when such stimulation is attended by defective root-supply or excessive evaporative loss of fluid. While the stimulation and functional activity of the protoplasts remain at a maximum, full turgescence is impossible in the absence of sufficient water-supply; and, when the supply falls beneath a certain limit, the degree of turgescence in the guard-cells is so lowered that they no longer possess the excess of functionally acquired strength sufficient to overcome the structural resistance of the surrounding tissue; and, when once this condition has been reached, closure of the orifices, or, in other words, an assumption of the nocturnal position, must take place. The guard-cells are from their position and structure specially exposed to evaporative loss, and are therefore specially liable to lose turgescence, in spite of their functional peculiarities, whenever the relations between root-supply and transpiratory loss of water are such as to imply a relative excess in the latter. They are thus liable to lose turgescence on diminished access of water to the roots, or on excessive evaporative loss determined by depression of atmospheric humidity; and, as a matter of fact, we know that the condition of the stomatic orifices does vary in relation to fluctuations in water-supply, quite apart from any fluctuations in degree of solar stimulation, and that it is precisely on their occurrence that one of the main functions of the stomata depends. The movements determined by variations in the turgescence of the guard-cells are sometimes connected with physiological and sometimes with purely physical causes, sometimes with variations in the functional activity of the guard-cells, and at others with variations in the relations of general supply and loss of fluid dependent on telluric and atmospheric conditions. In the one case we have the cell-sap becoming less retentive of fluid, due to diminished manufacture of osmotic products by the protoplasts; in the other, we have a deficiency in the amount of fluid which is available for retention, and in both cases the same ultimate result is arrived at, namely diminished turgescence. The closure of the stomata during the course of hot dry days is thus the parallel of the wilting of common leaves and the assumption of the nocturnal position in nyctitropic ones under similar conditions. All three phenomena are due to a loss in turgescence, which is determined, not by any diminution in protoplasmic stimulation, but by deficient water-supply to satisfy the osmotic capacities of the products arising in the cell-sap under the influence of solar stimulation.

CHAPTER VI.

The nyctitropic movements of leaves.

In the previous chapter we have found grounds for believing that the movements to which the opening and closure of the stomata are due depend primarily on certain structural and functional differences between the guard-cells and the other epidermal elements, and secondarily on the relations between general loss and supply of water determined by atmospheric and telluric conditions; and when we come to deal with the movements of entire leaves, whether these be of a nyctitropic nature or such as occur under conditions in which they are ordinarily regarded as the result

of active contraction of the protoplasts of the motor organs, we find abundant evidence that they are due to an essentially similar causation The movements in these cases being determined not by individual cells, but by masses of tissue, are often of very considerable magnitude and are thus more readily appreciable than the stomatic movements are, but, like the latter, they are determined either by fluctuations in the retentive power of the cell sap or by variations in the supply of fluid available for retention Accordingly we find them manifesting themselves either as the result of alterations in stimulation of assimilatory activity of the protoplasts of the motor organs, of variations in the relation of root supply to transpiratory loss, or of variations in conditions affecting filtration

The periodic assumption of the nocturnal and diurnal positions by nyctitropic leaves is a phenomenon of precisely the same nature as the coincident opening and closure of the stomata and the changes in colour of the fronds of *Selaginella serpens* in being essentially due to alterations in the osmotic properties of the cell sap but the action of these is affected by their coincidence with certain general relations of supply and loss of fluid Consequently, just as in *Selaginella* we find the maximum of whiteness in the fronds occurring in the first part of the night, so in the case of nyctitropic leaves we find the nocturnal position attaining its maximum at the same time The attainment of the maximum of the nocturnal condition at or shortly after sunset, and the occurrence of a reversion towards the diurnal one during the latter part of the night, are characteristic features in nyctitropic phenomena generally The maximum is attained at the time it is, because then the cessation of solar stimulation of assimilatory activity and the consequent loss in osmotic property of the cell sap coincide with unaltered, or inappreciably altered, relations between general loss and supply of water Depression of turgescence reaches its normal maximum whilst absence of solar stimulation and continued transpiration are acting coincidently to give rise to loss of fluid from the tissues, and, when one of the factors ceases to act, a rise in turgescence naturally follows, and in certain cases may even go so far as almost to re-establish the diurnal condition under normal circumstances During the day we have to deal with two opposing factors increased protoplasmic stimulation on the one hand, and increased transpiratory loss on the other At sunset we have two factors, decreased protoplasmic stimulation and continued evaporation, acting consentaneously to diminish turgescence After the dew point has been reached, there is a continued absence of solar stimulation, but this is no longer associated with transpiratory loss, and, the root-supply continuing as before, the cell sap is left at liberty to satisfy any osmotic capacities which it continues to have apart from the addition of special assimilatory products to it by the protoplasm under the influence of solar stimulation The absence of solar stimulation does not cause a complete cessation of protoplasmic activity or a total loss of osmotic property in the cell sap, as death of the tissue does in those cases in which the osmotic property is dependent on unstable compounds, it only gives rise to depression in them Absence of solar stimulation does not give rise to an abolition of functional activity, it merely implies withdrawal of one special stimulus to its exercise Even in the total absence of solar stimulation, therefore, a great degree of turgescence persists under normal relations of general supply and loss of fluid, and, where supply continues and loss is arrested, the turgescence may nearly attain the degree which it normally has when the tissues are exposed to coincident solar stimulation and normal transpiratory loss, and may exceed

that co-existing with the fullest solar stimulation and excessive transpiratory loss. A nyctitropic leaf at any time of night is normally in a very different condition from one which has been immersed in boiling water or exposed to the continued action of the vapour of chloroform. Maximum turgescence is only attained where full solar stimulation co-exists with free supply and abolished loss of water; but all degrees of turgescence short of this are constantly present in all ordinary tissues in relation to the varying conditions of protoplasmic activity and general loss and supply of water present in them under different circumstances. A greater degree of turgescence will naturally tend to be present where depression of functional activity coincides with an absence of transpiratory loss than where the latter is still actively going on, and hence we find the maximum departure from the diurnal state taking place at and shortly after sunset. With the arrest of transpiratory loss the osmotic capacities of the cell-sap are able fully to satisfy themselves. These, although not so great as they are under the influence of solar stimulation, are yet sufficient to cause the turgescence of the tissue to attain a higher degree than it attains under the fullest solar stimulation where the latter co-exists with excessive transpiratory loss and insufficient root-supply. In the study of movements dependent on alterations in turgescence, whatever their nature be, it must always be borne in mind that we are dealing with phenomena arising not as the result of the action of a single ultimate factor, but of the action ot various factors which may be associated with one another in very different combinations. Fluctuations in turgescence are capable of arising not only as the result of fluctuations in osmotic property of the cell-sap, but also in consequence of fluctuations in the relations between general supply and loss of water, or in the conditions of pressure, and therefore of filtrative loss to which the tissues are exposed.

All nyctitropic movements are in their origin essentially similar to the movements determining the opening and closure of the stomatic orifices. They are due to the presence of masses of tissue differing from one another in structural and functional property and so related to one another that they tend to give rise to displacements in opposite directions. Their structural and functional differences give rise to the occurrence of unlike fluctuations in their turgescence under the influence of like conditions, and therefore under the influence of varying conditions we find their relative strengths varying, and movement taking place in one or other direction accordingly. In the case of the stomatic movements, the motor apparatus—the guard-cells and the common epidermal cells—are in immediate relation to one another; but, in cases where movements of entire leaves or of large parts of leaves occur, the motor agents are generally so disposed as to tell on opposite aspects of masses of passive tissue whose displacement they make for. In the case of freely motile pulvini, for example, we find the motor apparatus consisting of thick masses of cortical parenchyma, around a cord of passive tissue consisting of modified wood and pith, or of the former alone. The precise disposition of the pads of cortical parenchyma in relation to the passive tissue on which they act varies in different cases; but we can always recognise them as consisting of two opposed sets, differing from one another in structural and functional properties and making for displacement of the passive tissue in opposite directions. In certain cases the relation of the opposing tissues, however, more closely resembles that which we find present in the case of the guard-cells and ordinary epidermal cells. The movements in the opposite halves of the laminæ of the pinnæ of many nyctitropic leaves at a certain stage of their evolution are effected under the influence of structural

arrangements of this type At a very early stage of development the two halves of the lamina have their upper surfaces closely applied to one another, whilst in the mature laminæ they are permanently expanded in the same plane, but an intermediate stage exists during which periodic diurnal and nocturnal movements of alternate expansion and approximation of the opposite halves take place Here there is no appearance of opposing masses of active tissue telling on an intermediate passive one, but the opposing tissues which determine movement are in direct relation to one another It is the growth of parenchyma over the line of the midrib which ultimately gives rise to permanent expansion of the lamina by forcing out the divergent woody bundles of the veins from their original direction, and which in the intermediate stage gives rise to periodic nyctitropic movements of the two halves in relation to variations in the degree of turgescence in the growing tissue under the influence of sunlight and darkness All that is necessary in order to the occurrence of nyctitropic movements is the presence of opposing tissue elements or masses of tissue, differing from one another in structure and function, and undergoing unlike fluctuations in turgescence under the influence of particular conditions.

The differences distinguishing the masses of tissue which make respectively for the diurnal and nocturnal position of entire leaves or large parts of leaves are of the same nature as those which we have already seen to distinguish the guard cells and the common epidermal elements The tissues making for the diurnal position are relatively late in development and rich in protoplasm, and specially in chlorophyll, as compared with those which make for the nocturnal position But relative youth and *abundance of protoplasm à priori imply relative structural weakness and functional* strength, and the presence of chlorophyll implies a special assimilatory exercise of the latter under the stimulant influence of sunlight Under the latter a greater rise in turgescence will thus take place in the masses of tissue which make for the diurnal position than in those making for the nocturnal one During exposure to sunlight there is a general rise in turgescence, but this is not uniformly distributed, but takes place to a greater extent in one of the opposing masses of tissue than in the other and the former thus becoming temporarily the stronger is able to determine displacement of the parts to which it is opposed Passive structural strength must, of course, remain unaffected by exposure to light or darkness, but the strength arising from functional sources is not constantly alike, but fluctuates with the degree of turgescence present at any given time Any tissue in which an excess of turgescence arises in connection with exposure to certain conditions must become relatively stronger than a tissue in which there is not an equal rise, the difference in strength being directly related to the difference in degree of turgescence Under the influence of solar stimulation we have greater assimilatory activity in the tissues making for the diurnal than for the nocturnal position But turgescence being directly related to assimilatory activity, this implies a corresponding excess in strength and a proportionate rise in capacity for resisting the pressure of opposing tissues, and consequently displacement of the latter occurs

Apart from solar stimulation and general transpiratory loss, the position of the various parts of nyctitropic leaves will be determined by the relative structural strength and permanent functional activity of the opposed tissues in the motor apparatus On the incidence of sunshine, structural strength remains unchanged, but an excess of functional strength—an excess of turgescence—arising in one of the opposed tissues, displacement must occur in direct proportion to the excess The amount of

displacement which actually occurs will, however, be affected by the conditions of general loss and supply of fluid; for the very tissues which provide for special rise of turgescence from functional causes are also those which present the greater structural facilities for transpiratory loss. In young tissues we have a relative excess of protoplasm providing for the presence of osmotic products in the cell-sap; but at the same time the facilities for loss of fluid in consequence of pressure or evaporation are greater than they are in older tissues in which the formed materials—the cell-walls—are more matured. Hence the fullest solar stimulation will be incapable of giving rise to the full assumption of the diurnal position, unless it be associated with certain conditions of general supply and loss of water. During the day, the precise position assumed by nyctitropic leaves will be determined partly by degree of solar stimulation, and partly by conditions of root-supply and evaporative loss. At sunset we have the removal of solar stimulation, but, under ordinary circumstances, no immediate cessation of transpiratory loss; and hence the position assumed by the leaves is not the neutral one determined by persistent protoplasmic activity apart from transpiratory loss; but passes beyond this, so as to reach a nocturnal maximum determined by the fact that the tissues in which the fall of functional activity is greatest are also those allowing most readily of transpiratory loss. Subsequently, as transpiratory loss diminishes and gradually disappears, the tissues will naturally acquire the degree of turgescence corresponding to the osmotic capacities of the cell-sap apart from the addition of assimilatory products under the influence of solar stimulation, and the tissues which make for the diurnal position will become relatively stronger than they were when subject to transpiratory loss. There will necessarily be a general rise in turgescence, but the rise will be greater in those masses of tissue which are most affected by transpiratory loss, and hence a reversion towards the diurnal position takes place. The fully developed diurnal position is not, however, attained until solar stimulation comes in to induce an excess of osmotic property in the cell-sap of the masses of tissue of greatest functional strength.

The actual amount of displacement occurring in individual cases is further affected by the arrangement of the opposing masses of tissue in the motor organs. In some cases, we find the masses making for the diurnal position so situated that they are aided by the action of the leverage of other parts of the leaf; in others, we find that, in addition to overcoming the action of their opponents, they have to oppose that of the leverage; and it is clear that, other things being alike, a greater displacement will be effected by the same rise in turgescence in the first instance than in the second. In endeavouring to account for the movements occurring in any individual case, therefore, the precise arrangement of the opposed masses of tissue in the motor organs must be considered not merely locally, but in relation to other parts of the leaf.

CHAPTER VII.

The structural peculiarities of the motor Organs of Nyctitropic Leaves.

In considering the question of the movements of stomata, it was pointed out that the elements which make for the diurnal position—the guard-cells—differ from the surrounding epidermal elements in certain features; we have now to endeavour to determine how

far differences of a like nature can be recognized in the case of nyctitropic tissu generally In the case of the guard cells, it was easy to show that we were dealing w elements characterized by their relative youth, functional strength, and structural weakn in certain directions, it now remains to ascertain how far similar distinctive features a present in the masses of tissue which make for the diurnal position in other examples nyctitropism

That the masses of tissue which make for the diurnal position of nyctitropic leav are younger than those making for the nocturnal one, is very clearly indicated in m cases by the fact that in the assumption of the nocturnal position there is a manif tendency to reversion to one which was a permanent position at a very early stage development of the leaf, or the diurnal one during an earlier portion of the period duri which movements occur In the leaves of most species of *Bauhinia* immediately befo movements begin to occur, the laminæ are depressed at angles of various degrees fr the line of the petiole and have their two halves folded up, so that their upper surfac are in close contact with one another When nyctitropic phenomena begin to appear, t laminæ rise and unfold during the day and sink and fold up at sundown (Plate Fig 6) In *Cassia alata* the pinnæ just before they become motile, are folded l Bauhinia leaves and have their midribs closely applied to the sides of the rachis a directed upwards and forwards at an acute angle to it When movements set in th consist of diurnal separation of the upper surfaces of the two halves of the laminæ a divergence and depression of the midribs, and of nocturnal folding of the laminæ a convergence and elevation of the midribs In *Cassia sumatrana* the pinnæ, immediate before they begin to show periodic movements, are disposed as in the previous speci save that their midribs, in place of being elevated, are deeply depressed beneath the pla of the rachis, and here we have diurnal unfolding of the laminæ accompanied l elevation and divergence of the midribs, and nocturnal folding coinciding with conve gence and depression In the leaves of *Pithecolobium saman*, which are ultimate characterized by the great development and persistence of their nyctitropic movement the permanent position of the various parts at a very early stage of development is follows The lower part of the primary rachis is directed at a very acute angle to th axis and the distal part is at first somewhat curved inwards (*vide* Plate I, Fig 13), an subsequently, as the weight of the secondary rachises and pinnules increases, abruptl curved outwards The secondary rachises are closely appressed to the primary one an are directed obliquely upwards and the pinnules are fully expanded and are related t the secondary rachises as the latter are to the primary one Somewhat later, as the woo strengthens the primary rachis straightens out, still retaining an acute angle to the axi The secondary rachises at the same time sink and are ultimately depressed beneath th plane of the primary one, whilst the pinnules retain their original arrangement Whe nyctitropic movements set in, they are not complicated by any folding and unfolding o the pinnules, as these are from the outset fully expanded, and the diurnal position i characterized simply by divergence of the primary rachis from the axis, divergence an elevation of the secondary rachises and depression of the pinnules, so that their surface come to look upwards and downwards in place of inwards and outwards. The entir series of pinnules on any secondary rachis here as in the case of many other bipinnat leaves, both in their original arrangement and in their movements, clearly corresponds t the lamina of one pinna in a pinnate leaf such as that of a *Cassia*, whilst in other case we find them each originally folded and exhibiting movements corresponding to those o

individual pinnæ. At sunset we find the primary rachis becoming extremely converged to the axis, sometimes indeed so much so that the upper portion actually crosses the line of the latter, the secondary rachises converging and sinking and the pinnules once more rising so as to bring their upper surfaces into close contact, and their midribs to assume a line directed upwards and somewhat forwards from the plane of the secondary rachis to which they are attached. Here every part of the leaf from the primary rachises to the pinnules moves, and in doing so, diurnally departs from, and nocturnally reverts to, what was the permanent position at an earlier stage of evolution.

In the case of *Mimosa pudica*, as in that of *Pithecolobium saman*, extensive periodic movements take place in all parts of the leaves. Immediately before they begin to occur, the permanent position is as follows:—The primary petiole is widely divergent from the axis, the secondary petioles are closely converged to one another, and either follow the line of the primary one, or ascend slightly from it, whilst the pinnules are, as they have been from the outset, fully expanded, and have their midribs closely conveyed to the line of the secondary rachises and directed upwards and forwards, so that the upper surfaces of the laminæ of the opposite members of the series are in immediate contact. When movements are established, they consist of diurnal convergence of the primary petiole towards the line of the axis, diurnal divergence of the secondary rachises from one another, and diurnal divergence, depression, and a certain amount of rotation of the pinnules, so that their midribs come to be more or less in the same plane with, and at right angles to, the secondary rachises, and their superior and inferior surfaces to look directly upwards and downwards, alternating with nocturnal divergence of the primary petiole from the axis, nocturnal convergence of the secondary rachises to one another, and nocturnal reversion of the pinnules to their embryonic position. The movements in *Mimosa pudica* and *Pithecolobium saman* are thus essentially similar in their nature, in that in every part of the leaves they involve a diurnal departure from, and a nocturnal reversion to, a previously permanent position. They differ, however, in detail, because in the one case the latter implies divergence and in the other convergence of the primary petiole in relation to the axis. This in no way affects the question of the nocturnal position being one of reversion, but the difference is at the same time important, because it implies a great difference in the stability of the diurnal position in the two cases. The diurnal position is in any case an unstable one, depending as it does on a temporary victory of functional over passive structural resistance; and it is evident that in an instance like *Mimosa pudica*, in which the diurnal position of the primary pulvinus implies that the mass of tissue making for it must overcome not merely the resistance offered by the opposing part of the pulvinus, but also that of the leverage of the distal parts of the leaf, the instability must be greater than where leverage and special rise in turgidity, due to functional causes, co-operate in determining the position. In *Pithecolobium* the mass of pulvinar tissue in which functional activity preponderates lies above the flexible fibro-vascular axis of the main pulvinus, whilst in *Mimosa pudica* it lies below it. The diurnal excess in turgescence in the one case makes for divergence and in the other for convergence of the petiole. But the weight of the distal parts of the leaves is constantly making for divergence, and especially so during the day, owing to the increase in turgescence and weight which takes place under the influence of solar stimulation of functional activity. In *Pithecolobium*, therefore, the diurnal relative increase in strength of the functionally stronger pulvinar tissue, and the increased leverage of the distal parts of the leaf coincide in making for divergence of the petiole, whilst in *Mimosa pudica*

the pulvinar tissue makes for convergence and the distal parts of the leaf for divergence Under these circumstances, it need not surprise us to find conspicuous changes in the position of the leaves of *Mimosa* taking place under the influence of factors affecting pulvinar turgescence which are incapable of producing any appreciable results in the case of the leaves of *Pithecolobium*

In some cases, as in the pinnules of *Pithecolobium saman* and *Leucæna glauca*, the movements during a great part of the life of the leaf effect a complete nocturnal restoration of what was a permanent position at an early stage of evolution, and when they cease to do so, determine a simple incomplete restoration, but in other cases, as time goes on, the development and increased strength of certain masses of tissue introduce complications, and we no longer find simple complete or incomplete restoration taking place In the pinnules of *Pithecolobium* and *Leucæna glauca* we are dealing with laminæ which from the outset are fully unfolded, and the movements which they exhibit are simply due to the subsequent development of a mass of parenchyma over the insertion and base of the midrib, which, when its turgescence rises under the influence of solar stimulation, is able to determine the divergence and depression of the lamina But in cases, such as the pinnæ of *Cassia alata* where the lamina is primarily folded and shortly afterwards becomes permanently expanded, the characters of the movements become modified when the latter condition has been established, factors which previously determined expansion or folding of the lamina now coming to determine movements of rotation in it This modification of movement may be more satisfactorily dealt with in considering the particular phenomena presenting themselves in individual leaves, and is merely alluded to here in order to indicate that we may not in all cases be able at once to recognize that the nocturnal position corresponds to a reversion to an originally permanent position In all cases it corresponds to a tendency to such reversion, but the degree and simplicity with which the process is carried out is often greatly affected by structural modifications which have been established subsequently to the period at which the primary permanent position was first departed from

The fact that the masses of tissue making for the diurnal position of the various parts of nyctitropic leaves, agree with the corresponding elements determining the diurnal condition of the stomata in being relatively young, is thus indicated by the characters of the movements which they give rise to, but we are fortunately not obliged to remain satisfied with evidence of this nature, as in many instances we find most conspicuous structural indices of the same fact Figures *a* to *g*, Plate I, Fig 14, show the appearances presented by the primary pulvini of seven successive leaves on a shoot of *Pithecolobium saman*, and in passing from 1, which is the youngest, to 7, which is the most mature member of the series, the excessive development of the mass of tissue on the upper aspect of the pulvinus during the later stages of evolution comes out most distinctly The evidence afforded by sections through the thickness of pulvini of different ages is equally convincing, for these show that at first the development of the superior pulvinar pad lags behind, and at a later stage overtakes that of the inferior one (Plate I, Fig 15, Plate IV Figs 1, 2) So, in the case of the tertiary pulvini, the superior pad is at first very inconspicuous, but ultimately appears as a prominent mass of vivid green tissue In cases where, as in the primary pulvini of *Cassia alata*, the fibro vascular tissue does not assume the form of a simple unlignified central cord, but remains arranged in a ring and undergoes normal processes of lignification, conspicuous periodic movements do not manifest themselves, and the continued growth

of the upper or axillary pad during the later stages of the evolution of the leaf merely serves to aid the increasing leverage of distal parts in determining a gradual and progressive increase in divergence from the line of the axis. In such cases the arrangement and character of the vascular bundles of the pulvinus are such that mere fluctuations in turgidity are unable to give rise to corresponding displacements of the petiole, and it is only as the result of continued growth that the degree of divergence is determined.

There is thus both dynamical and structural evidence that the masses of tissue in the motor organs which make for the diurnal position are younger, or contain a larger number of young elements, than those which make for the nocturnal one; and this in itself almost necessarily implies that, as a whole, they are structurally weaker and functionally stronger than the latter are. Taking any ordinary unit of vegetable tissue, there can be no doubt that, as a rule, the proportion of active protoplasm in it tends to diminish, and that of formed material to increase, with increased age. The formed material may take the shape of secretions of various kinds, or may enter into the constitution of the cell-wall. In any case there is a tendency to diminution in the relative amount of protoplasm, and, in cases where continued additions are made to the cell-wall, these imply increased structural strength, and hence, speaking generally, the larger the number of young elements in any tissue, the greater will its functional power be; and the larger the number of old elements, the greater its structural power. It follows from this that in pulvini in which we have to deal with opposing masses of tissue differing from one another in regard to the period during which active growth continues, we are necessarily dealing with an opposition of functional and structural strength, the less mature tissue being functionally, and the more mature structurally the stronger. But the effect produced by exposure to stimulation must be proportionate to the amount of material to be stimulated; and hence, under exposure to any conditions implying protoplasmic stimulation, the functionally stronger tissue will undergo a greater increase in activity than the structurally stronger one, and where the increased activity leads to increased turgescence, as that induced by solar stimulation unequivocally does, it will undergo a corresponding increase in relative strength. Under solar stimulation a general increase in turgesence takes place, but this is not equally distributed; and, the increase being greater in the structurally weaker tissue, this fact gives it a temporary advantage and enables it to overcome the resistance in the structurally stronger one, which determines the position apart from solar stimulation. The cord-like arrangement of the fibro-vascular tissue, and the absence of lignification in typical pulvini, provide facilities for the action of the opposed masses of parenchyma on one another, and periodic movements consequently arise in connection with fluctuations in turgescence coinciding with the incidence or removal of solar stimulation.*

The masses of tissue which make for the diurnal position are not merely richer in protoplasm, and, therefore, endowed with greater general functional activity than

* Sachs (Vorlesung xxxvi, s. 775) accepts Millardet's and Pfeffer's statements that the pulvini do not lose but gain in turgescence under the influence of darkness, because their rigidity is increased then. But mere increased rigidity, even if it be actually present, is no conclusive evidence of increased turgescence, as it may merely indicate that the tissues have passed into a condition of more stable passive equilibrium than they possess under the influence of light, and the fact that an assumption of the nocturnal position follows defective supply or excessive loss of water seems conclusively to show that it is connected with decreased turgescence in the motor organs. In the case of the stomata in which the condition of the motor apparatus can be made the subject of direct observation, and in which the movements occur under precisely the same conditions as they do in nyctitropic leaves, we do not find darkness giving rise to increased but to decreased turgescence in the active elements.

their opponents, but are also as a rule specially richer in chlorophyll, and therefore specially subject to the influence of solar stimulation as a source of increased turgescence dependent on the manufacture of assimilatory products This in many cases, as in those of the pinnal pulvini of *Cassia alata*, and in the secondary and tertiary pulvini of *Pithecolobium saman*, is evident to the most cursory inspection owing to superficial differences in colour, and in all it can be readily ascertained by means of microscopic sections, especially if these have been momentarily immersed in a 2 per cent solution of osmic acid so as to fix the colouring matter in the chromatophores (Plate I, Figure 19, Plate II, Figs 3, 5—8, Plate IV, Figs. 3, 5—9)

The diurnally dominant tissues in the pulvini of nyctitropic leaves are then distinguished from the nocturnally dominant ones by precisely the same features which distinguish the guard cells of the stomatic orifices from the common epidermal elements

They are distinguished by their youth, or by the large proportion of relatively young elements which they contain, by their relative structural weakness, and by their relative functional strength, especially in relation to solar stimulation, and the movements which they give rise to are of essentially similar origin to those caused by the guard cells Just as the guard cells are able to effect a displacement of the surrounding tissue when exposed to sunlight because of their temporary excess in turgescence, so are the masses of tissue in the pulvini which make for the diurnal position able to effect displacement of their opponents under similar circumstances The condition of the stomatic orifices is regulated not merely by fluctuations in the degree of solar stimulation to which the tissues are exposed, but also by the coincident conditions of root supply and transpiratory loss of water, and the same holds good in regard to the position of nyctitropic leaves Where transpiratory loss is in excess, and yet falls short of the degree necessary to cause general wilting of the tissues, we find both stomatic orifices and nyctitropic leaves assuming the nocturnal position, and in both cases a resumption of the diurnal one follows a restoration of the normal relation between general loss and supply of fluid, whether this be attained by means of diminished transpiration or increased root supply The excess of functional activity in the guard cells, and the masses of pulvinar tissue making for the diurnal portion, provides that they shall undergo a greater increase in turgescence under solar stimulation than their opponents do, and thus implies a temporary increase in the resistance which they present to them, but at the same time the excess of structural strength in the common epidermal elements and the pulvinar tissues making for the noctural position gives them a relative protection from the action of conditions implying an excess of transpiratory loss over root supply of water The result of this naturally is that, where this excess rises high enough, a resumption of the nocturnal position occurs in spite of the continued stimulation of the more active tissues, because these are no longer able fully to satisfy their osmotic capacities Where conditions of general supply and loss of fluid hold a normal relation to one another, the diurnal position is secured by the greater osmotic capacity of the more active tissues, but as these are also structurally weaker ones, they are the first to suffer from loss of turgescence connected with insufficient supply

Stomatic movements are specially distinguished by their persistence and constancy of character Once established, they continue to occur with constancy and regularity

so long as the tissues retain their vitality, but this is by no means the rule with other nyctitropic movement. In certain cases we do find the latter retaining a uniform character throughout, but in most cases they undergo considerable modification in regard to their precise nature, and especially in regard to their extent as time goes on, and in many cases we find them almost or entirely absent during considerable periods in the latter part of the life of the leaves in which they once were conspicuously present. As we have already seen, they only begin to manifest themselves after the evolution of the leaves has reached a certain point, and subsequently we find them, as a rule, rapidly increasing in amount, attaining a maximum, and then declining from this to a greater or less extent. The various parts of the leaf are primarily in a condition of stable equilibrium; this is succeeded by one of unstable equilibrium which gradually attains a maximum and then declines from this towards, or absolutely to, renewed stability. The position of the various parts of any leaf is necessarily determined by the structural peculiarities and degree of turgescence which they possess. Structural peculiarities are necessarily liable to modification with increasing age, but at any particular time they may be regarded as fixed factors. This is not, however, the case in regard to conditions of turgescence which are liable to undergo constant fluctuations in connection with variations in protoplasmic stimulation and activity, and fluctuations in the relations between root-supply and transpiratory loss. Where all the tissues are subject to like fluctuations in turgescence, mere alterations in their consistence culminating in one direction in free excretion of water, and in the other in general wilting will occur, but no definite movements will present themselves. It is only when special masses of tissue, differing from one another in their capacity for, and liability to, fluctuation in turgescence are present that orderly, definite movements will occur, and then only in association with certain structural peculiarities. Nyctitropic movements, therefore, only present themselves after leaves have attained a certain stage of development, and in connection with the evolution of specially situated masses of tissue, so disposed as to provide an active opposition between structural and functional factors, and it is only so long and so far as the differences in structural and functional properties of these masses persist that movements will occur. The relative youth of the masses of tissue making for the diurnal position at first provides that the difference shall be very considerable, and movements are accordingly very conspicuous for a time, but as in most cases, at all events, this difference naturally tends to diminish with the increase in structural strength and expenditure of active protoplasm of the younger tissues, a condition of stable equilibrium is once more approached or actually attained with a corresponding diminution or abolition of movement.

Great differences occur in regard to the rate at which the movements, whether of a normal periodic character or arising as the result of extrinsic agencies affecting filtration or water-supply, are carried out in different leaves, the rate bearing no definite relation to the magnitude of movement, but being related to structural features affecting the redistribution of fluid throughout the tissues The movements are primarily due to fluctuations in the osmotic properties of the cell-sap, to fluctuations in external pressure, or to fluctuations in water-supply, giving rise to corresponding alterations in the degree of turgescence of the various parts of the motor organs; but the rate at which these alterations can be effected must necessarily be influenced by the structural features of the walls of the cells entering into the constitution of the

tissues as favouring or obstructing the access or escape of fluid Taking any highly turgid cell, in which a great fall in the osmotic capacity of the cell sap sets in, a proportionate loss in turgescence must ultimately ensue owing to the filtrative discharge caused by the elastic recoil of the cell walls, but the rate at which the discharge is conducted must be regulated by the facilities which the latter provides for filtration, and by the degree to which ready accommodation for the escaping fluid is present This being so, the rate at which movements occur ought to bear a recognisable relation to the degree of pitting of the cell walls and to the openness of the pulvinar parenchyma, and direct evidence that this is actually the case is not wanting The movements which are executed by the pinnæ of *Cassia alata* are certainly, in so far as magnitude is concerned, fairly comparable with those occurring in any part of the leaves of *Mimosa pudica*, but the rate at which they are conducted in the two cases is very different, the movements in the former being very slowly carried out as compared with those in the latter Coinciding with this difference in rate of movement we find very conspicuous differences in the structural details of the pulvini, the pulvinar tissue in *Cassia alata* being throughout dense and composed of cells which are provided with only a limited number of small pits, whilst in *Mimosa pudica* the deeper strata of the tissue are not only very open in texture, but are composed of elements characterised by an abundance of huge pits (Plate VI, Figs 3, 4, 12)

The facilities for filtration must evidently bear a direct relation to the extent to which the cell walls are pitted, and where extensive pitting is combined with very considerable thickness and strength of the cell walls elsewhere, as it is in the primary pulvini of *Mimosa pudica*, filtratice facilities naturally attain a maximum (Plate VI, Figs 3, 4, 12, Plate VII, Fig 5) In the case of the movements occurring in the leaves of *Leucœna glauca* and *Cassia sumatrana*, we also find very clear evidences of a correspondence between rate of movement and textural facilities for filtration The movements in *Leucœna glauca* are relatively rapid, those in *Cassia sumatrana* comparatively slow, and coinciding with this we find the pulvinar parenchyma much more conspicuously pitted in the former than in the latter case (Plate VII, Figs 2, 4)

It is clear that turgescence must be maintained with greater difficulty where filtrative facilities are great than where they are small, and consequently that the stability of any position maintained as the result of the active turgescence of a mass of tissue must vary inversely with the filtrative facilities which the latter provides This being so, we have reasons to conclude that, where filtrative facilities are great, we ought to find conspicuous movements occurring under the influence of conditions which are incapable of inducing such results where filtrative facilities are relatively small It need not, therefore, surprise us to find conspicuous movements occurring in the leaves of *Leucœna glauca*, and even more in those of *Mimosa pudica* under conditions in which no appreciable movements occur in those of *Cassia alata* and other similar leaves A single rough breath of wind will, under favourable circumstances cause a certain amount of alteration in the relative position of the various parts in the leaves of *Leucœna glauca* and very extensive alterations in those of *Mimosa pudica*, but the agitation necessary to secure perceptible displacement in the leaves of *Cassia alata* or *Cassia sumatrana* must be frequently repeated. The disturbance to which the leaves are primarily subject by the wind may be the same, and may in all cases give rise to like increase in the external pressure to which the turgid pulvinar tissues are exposed, but the amount of fluid actually discharged from the cell cavities under its influence must

vary with the structural facilities provided for filtration. The pulvinar tissues in *Leucæna glauca*, and especially in *Mimosa pudica*, provide great facilities for filtration; their pulvinar turgescence is consequently very unstable, and movements are very readily induced in them; whilst in *Cassia alata* the tissues provide minor facilities, and must be subjected to frequently recurring increments of external pressure before a sufficient filtrative displacement has occurred to cause alterations in turgescence of sufficient magnitude to lead to appreciable alterations in the relative positions of the various parts of the leaves.*

Parallel phenomena present themselves in cases where the tissues, in place of being exposed to conditions tending to give rise to increased filtration, have their normal water-supply interfered with. If a shoot of *Leucæna glauca* or *Mimosa pudica* be gently detached from the axis with a careful avoidance of all agitation likely to induce increased pulvinar pressure and consequent augmented filtrative loss, the precaution does not under normal circumstances prevent the leaves from manifesting movements, very rapidly in the former and almost immediately in the latter case; whereas in *Cassia alata* movements make their appearance only very gradually, and after the lapse of a considerable interval. In all cases the deprivation of water-supply under such circumstances is alike, but the rate of movement subsequent to its incidence varies according to the activity with which filtrative processes are normally carried on by the pulvinar tissues. The filtration which is constantly going on in the pulvinar tissues of *Leucæna glauca* and *Mimosa pudica* under normal circumstances is more rapid than in those of *Cassia alata;* and consequently when the water-supply is cut off the turgescence of the tissues in the former cases falls more rapidly than it does in the latter one.

The degree of turgescence in any mass of tissue at a given time must necessarily depend on its osmotic capacity and on the supply and filtrative loss of fluid to which it is subjected. The condition is one of unstable equilibrium, and the degree of instability must necessarily be related to the degree to which inherent filtrative facilities are present. Where these are present in high degree, any diminution in osmotic power, any increase in conditions of external pressure, or any arrest in the supply of fluid available for absorption, will give rise to proportionately rapid loss in turgescence. Where, on the other hand, they are low, the loss must necessarily be correspondingly delayed. Turgescence implies a balance between certain conditions of osmotic gain and filtrative loss of fluid, and any decrease in the former or increase in the latter must necessarily tend to give rise to diminished turgescence. Decreased absorption may arise either as the result of decreased osmotic property or of decrease in the amount of fluid available for absorption, and increased filtration must tend to arise under the influence of any augmentation of external pressure. The structural facilities for filtration, however, remain constant, and consequently the alterations in turgescence which actually take place under the influence of any alterations in the conditions to which a mass of tissue is exposed must necessarily differ in different instances, their magnitude and the rate at which they are capable of inducing appreciable movements varying with the structural peculiarities of the affected tissue.

* According to Sachs (Vorlesungen XV, s. 302) mere agitation not improbably raises transpiratory loss from the leaves; but such increased loss cannot be the essential determinant of the alterations in turgescence of the motor organs alluded to above, as we find the assumption of the nocturnal position occurring equally readily where the wind is accompanied by heavy rainfall, or as the result of agitation by the latter alone.

CHAPTER VIII

The nyctitropic movements of particular leaves in relation to the structure and arrangement of the tissues in their Motor organs The movements of the Leaves of Cassia alata and Cassia Sumatrana

In the course of the preceding chapter, an attempt has been made to show that the occurrence of nyctitropic movements generally is dependent on the presence of opposing masses of tissue situated in the motor organs and differing from one another in functional and structural strength If this be actually the case, it ought to be possible to show that some definite relation exists between the special movements exhibited by the leaves of particular plants and certain peculiarities of structural detail and arrangement in the tissues of their motor organs In attempting to do this, the best course appears to be to take a certain number of individual leaves and consider the peculiarities of their movements and the structure of their motor organs in detail

The leaves of *Cassia alata* afford specially favourable opportunities for study, because of their large size and the highly developed and complicated movements which they exhibit Fully developed leaves in this species have from nine to twelve pairs of practically sessile pinnæ, the lowest pair being of relatively small size and inserted close to the base of the leaf and at a considerable distance from the next pair During the period in the life of a leaf in which movements are at a maximum, that is, in fully developed but still comparatively young leaves, the diurnal and nocturnal positions of the pinnæ are as follows —Diurnally their superior and inferior surfaces look directly upwards and downwards and lie approximately in the same plane with the upper face of the rachis their midribs at the same time diverging almost at right angles to it (Plate II Fig 1) In the early part of the night, on the other hand, the upper and under surfaces of the laminæ look directly inwards and outwards in a plane at right angles to the upper face of the rachis and the midribs are closely convergent and directed downwards at an acute angle to it (Plate II, Fig 2) It is clear that the movements which lead to the alteration of these positions must consist of alternating convergence and divergence of the midribs of the pinnæ, combined with excessive rotation in opposite directions and a certain amount of elevation and depression

If we watch the actual progress of the transition from the diurnal to the nocturnal position, we find that the first indication of displacement lies in a certain degree of elevation of the lamina, so that its upper surface slopes upwards from the plane of the rachis At the same time the divergence of the midribs gradually decreases The general elevation of the lamina is succeeded by steadily increasing elevation of its posterior or outer half over the level of the anterior or axillary one, which necessarily implies corresponding rotation of the midrib Rotation and convergence now advance simultaneously until the upper surface of the lamina has moved through a quadrant and the midrib has converged so greatly that the upper surface of the opposing members in each

pair of pinnæ are in close contact with one another and with the lateral surfaces of the rachis. Up to this time the midrib remains somewhat elevated at an acute angle to the plane of the rachis, but subsequently depression gradually sets in, so that the posterior and anterior edges of the lamina come in the first place to lie respectively horizontally superior and inferior, and ultimately to be directed downwards and forwards at angles of varying degree of obliquity from the line of the rachis. (Plate II, Fig. 2.)

The motor organs which determine this complicated series of movements are highly developed and present certain peculiarities which greatly facilitate a comprehension of their action. Both superficially and in section it is at once evident that they are composed of two distinct masses of tissue, one of which is of a warm ochreous and the other of a vivid green colour, and that these hold certain definite positions in relation to the deeply keeled vascular bundle of the pulvinus, and to the under and upper surfaces of the base of the outer half of the lamina. The ochreous tissue lies beneath and to the outer side of the vascular bundle and spreads out thence over the under surface of the base of the outer half of the lamina so as to involve and conceal the origins of the lowest four or five ribs. The green tissue, on the other hand, lies internally and superior to the vascular bundle and forms an expansion over the base of the upper surface of the outer half of the lamina. The disposition of the two masses of tissue is clearly shown in Figure 19 of Plate I and Figure 3 of Plate II, and the laminar expansion of the ochreous tissue in Figures 4 and 5 of Plate II. We have thus to deal with two distinct masses of pulvinar tissue: one intero-superior, the other extero-inferior, in relation to the pulvinar vascular bundle and the base of the outer half of the lamina, and differing greatly in the amount of their chlorophyll content. Now, it is clear that any alterations in the relative strengths of masses of tissue so disposed around a central, flexible axis must tend to give rise to movements of divergence or convergence, combined with varying degrees of depression or elevation and of rotation in one or other direction, according as the alteration implies increased strength in one or the other mass (Plate VII, Fig. 6). Were they merely related to the axial bundle they would give rise only to divergence or convergence, depression or elevation, and we should have movements similar to those which we find manifesting themselves in the secondary petioles of many bipinnate leaves; but the movements are in this case farther complicated by rotation, because they represent the outcome of forces which in the case of bipinnate leaves are distributed between the secondary petioles and the pinnules. The rotation of the axial bundle is determined by the relations which the opposed masses of pulvinar tissue hold to the inferior and superior surfaces of the rigidly expanded lamina. The ochreous infero-external mass is expanded over the base of the inferior surface of the outer half of the lamina, whilst the green intero-superior one holds a corresponding relation to the upper surface of the same area, and consequently any increase in strength in the former mass must tend to elevate, and any increase in strength in the latter mass must tend to depress, the outer half of the lamina, and therefore to cause corresponding inward or outward rotation or torsion of the flexible vascular bundle. Were the lamina not rigidly expanded, we should have had movements of elevation and convergence of the midribs and folding up of the outer half of the lamina alternating with movements of divergence and depression of the midrib and expansion of the lamina; and as a matter of fact such movements do actually occur at a particular period in the life of the pinna. When, however, the lamina becomes rigidly and permanently expanded, the factors which previously gave rise to movements of folding and unfolding do not cease to exist, but

their action is now expended in producing general rotation of the lamina and corresponding torsion of the flexible vascular axis of the pulvinus Had the pulvinar pads been disposed inferiorly and superiorly, we should have had simple elevation and depression, had they been external and internal simple convergence and divergence, but because they actually are extero inferior and intero superior and related respectively to the under and upper surfaces of one half of the lamina only, we have rotation taking place and modifying the character of the movements and the position which they ultimately give rise to

From the nature of the diurnal and nocturnal positions of the pinnæ, it is clear that during the day the intero superior and during the night the extero inferior pulvinus must possess a relative excess of strength, and the conspicuous differences in colour which they exhibit renders it easy to comprehend why this should be the case Even the most cursory examination in this case shows that the intero-superior pad is much richer in chlorophyll than its opponent This implies a proportionate excess in functional activity, and therefore of turgescence, under the influence of solar stimulation But increased turgescence implies increased strength and resistance in the tissue in which it occurs, and consequently the intero superior pad must necessarily acquire a relative increase in power during the day which enables it temporarily to overcome the action of its opponent

Movements of rotation which are so frequently present in high degree in the case of the pinnæ and pinnules of nyctitropic leaves are absent or inconspicuous in the case of their primary and secondary petioles, because in them the motor apparatus has no horizontal surfaces like those of the laminæ to act upon Where such surfaces are present, and the opposed masses of tissue are specially related to them, the action of the factors which in the case of the petioles give rise to simple convergence and divergence, elevation and depression is partially expended in determining various degrees of rotation In the present instance rotation advances so far that the outer half of the lamina, and the outer side of the keel of the midrib come to lie directly upwards, which of course implies that the basal laminar expansion of the extero inferior pulvinar pad lies to the upper side of the base of the midrib It is now incapable of giving rise to any further rotation, and its remaining power is expended in producing lateral pressure on the outer, and, for the time being, upper side of the keel of the midrib and proportionate depressive flexion in it

The alternation of the diurnal and nocturnal positions is not caused by alternating diurnal decrease and nocturnal increase in the absolute strength of the extero-inferior mass of pulvinar tissue, but by alternating diurnal increase and nocturnal decrease in that of the intero superior one There is nothing to show that any rise in turgescence of the mass of tissue making for the nocturnal position attends removal of solar stimulation On the contrary, we find the same position appearing under the influence of exposure to excessive transpiratory loss, and in leaves which are detached from the axis, and therefore subjected to entire arrest of water-supply The position is thus clearly one attending general loss and not any localised rise in turgescence On the removal of solar stimulation, a general loss of turgescence, and consequently of strength, takes place throughout the whole pulvinus but the loss is greatest in those portions which make for the diurnal position, because they are physiologically stronger and structurally weaker than their opponents The result of this is that, although the

latter become absolutely weaker in the absence of insolation, they at the same time become relatively stronger than they were before, and the previously existing equilibrium being proportionately disturbed, movements necessarily occur until a new position of equilibrium has been established.

As we have just seen, the nyctitropic movements of the pinnæ of *Cassia alata* are very extensive and highly complicated at a certain period in the life of the leaves. They are, however, entirely absent in very young leaves, and gradually diminish and disappear in mature ones long before these begin to show any other signs of loss of vigour. On their onset they make their appearance first in the basal pinnæ and gradually extend thence outwards along the course of the petiole. In leaves at the period when movements are just beginning to appear, all the pinnæ save the basal ones have the two halves of their laminæ permanently folded up, with their upper surfaces in close contact with one another, and the midribs directed upwards and forwards from the plane of the petiole. The distal pairs of pinnæ are in close contact with one another and with the sides of the petiole, whilst the proximal ones are more or less divergent, the divergence increasing in passing downwards towards the base of the rachis. In the youngest pinnæ there is as yet no sign of any accumulation of pulvinar tissue. The midrib lies in a groove on the upper surface of the lamina, and the basal ribs of the outer side of the latter emerge clean and clear from it. In the basal pairs of pinnæ the laminæ are partially unfolded during the day, the surfaces of the outer half being still almost vertical, but those of the inner one lying nearly horizontal. Their midribs are still directed forwards and upwards from the plane of the petiole, but much less so than those of the distal pinnæ. There is already a conspicuous mass of ochreous pulvinar tissue on the outer side of the keel of the midrib, and extending thence over the bases of the lower ribs on the under surface of the outer half of the lamina. As yet there is very little accumulation of green pulvinar tissue on the inner side of the keel, but a mass of it has begun to appear over the base of the upper surface of the laminæ and to extend outwards along the groove of the midrib. The diurnal position at this period is due to the following agencies:—The divergence is caused by the presence of a certain amount of green axillary pulvinar tissue, the partial unfolding to the commencing accumulation of pulvinar tissue over the base of the upper surface of the lamina and along the groove of the midrib, and the persistent elevation of the outer half of the lamina to the excessive development of pulvinar tissue over the bases of the lower ribs on its under surface. As time advances, diurnal divergence goes on steadily increasing with the increased development of axillary pulvinar tissue; expansion of the lamina becomes complete as the mass of tissue on the upper surface of the base of the outer half of the lamina increases in proportion to the earlier developed mass on the under surface, and permanent as the tissue over the upper surface of the midrib increases in amount and structural strength. For a long time, however, such structural and functional differences are present between the earlier and later developed masses of pulvinar tissue, making respectively for the nocturnal and diurnal positions as to give rise to nocturnal and diurnal fluctuations in their relative strengths of sufficient magnitude to induce extensive movements. After a time the functional strength of the axillary superior pulvinar tissue gradually decreases, whilst its structural strength simultaneously increases, so that the differences originally existing between it and its opponent progressively diminish and ultimately disappear, and after this, although general turgescence

continues to undergo diurnal and nocturnal fluctuations so long as the leaf retains its vitality unimpaired, these are no longer accompanied by displacements of the pinnæ, because they now affect the entire pulvinus alike in place of occurring in excess in particular portions of it

The movements of the pinnæ in *Cassia alata*, although so extensive and complicated when at their maximum, are always carried out comparatively slowly Owing to this we find that the leaves have hardly begun to show appreciable displacement of their pinnæ at a time in the evening when those of *Mimosa pudica, Leucæna glauca* and *Pithecolobium saman* have already completely assumed the nocturnal position Correspondingly they hardly show any appreciable movement under disturbances by wind or rain which suffice to cause complete movements in the leaves of these plants, and, on being detached from the axis, in place of immediately showing the effects of arrested water supply as the leaves of *Mimosa pudica* and *Leucæna glauca* do, they only slowly and gradually assume the nocturnal position This retardation of movement is the consequence of the structural features of the pulvinar tissues The masses of pulvinar parenchyma are dense, the intercellular spaces are very small, and the cell walls are provided only with few and small pits, and consequently any filtrative escape of fluid from the turgid cells whether it be of a normal character or the result of loss of osmotic capacity in the cell sap, or of rise in external pressure, can take place only gradually and slowly. In order, therefore, to give rise to any appreciable movements, the causes of increased filtration or of obstructed water supply must continue to act for a much longer time than it is necessary that they should act in cases where filtrative facilities are present in high degree

The pinnæ of *Cassia sumatrana* also exhibit nyctitropic movements which, although neither so complicated nor so persistent as those of *Cassia alata*, are very conspicuous during a certain period in the life of the leaves Fully developed leaves have from nine to twelve pairs of pinnæ, which differ from those of *Cassia alata* in certain important respects In place of being practically sessile, they are provided with distinct secondary petioles measuring 0 12″×0 04″, and they never possess conspicuous laminar expansions of pulvinar tissue (Plate III, Fig 4) Nyctitropic movements are very extensive in young leaves after they have attained a certain degree of development, but they very soon diminish in amount, altering in character as they do so, and are practically absent during the greater part of the life of the leaves Owing to the very transitory character of the movements, the nocturnal positions of the successive pairs of pinnæ in one and the same active leaf are by no means so uniform as they are in the case of *Cassia alata*, the distal, latest developed pinnæ often exhibiting the maximum of movement at a time when the movement in the basal ones has already undergone great diminution As usual, nyctitropic movements are entirely absent up to a certain period, after this they begin to manifest themselves with rapidly increasing intensity, very soon attain a maximum, and then rapidly decrease and disappear

In pinnæ in the earlier stages of development the halves of the laminæ are permanently folded up and in close contact with one another, and the midribs are slightly divergent and somewhat elevated from the plane of the common petiole, their keels at the same time facing directly outwards, so that the edges of the folded laminæ of opposite pinnæ are in close relation to one another (Plate III, Figure 1) At this period there is no evidence of any accumulation of pulvinar tissue in the secondary petioles

Somewhat later, and just before nyctitropic movements begin to appear, the folded pinnæ still remain only very slightly divergent, but in place of being elevated they are now permanently depressed, the midribs sloping downwards and forwards from the line of the primary petiole and having their keels directed downwards in place of outwards (Plate III, Fig. 1). The secondary petioles now show distinct evidence of an accumulation of pulvinar parenchyma over the anterior surface basally and along the entire length of the outer surface. Movements soon begin to appear and to lead to gradually increasing diurnal elevation, divergence and expansion of the pinnæ, alternating with nocturnal depression, convergence, and folding up of the laminæ. Somewhat later the laminæ become permanently expanded, and at the same time alternating movements of divergence and elevation and of convergence and depression go on increasing in amount. At this period the pinnæ during the day are widely divergent, and have their upper surfaces approximately in the same plane as the upper surface of the rachis (Plate III, Fig. 4), and at night are very closely convergent and depressed so greatly that their upper surfaces are vertical to the line of the rachis and look directly forwards towards its apex. The nocturnal position at this stage may be regarded simply as the result of extreme convergence and depression without any appreciable rotation. Rotation of the lamina, however, soon sets in and, for a time, goes on gradually increasing until, for a period, the upper surfaces of the pinnæ come to look directly inwards facing one another. This is the period at which the movements attain their maximum development, and it is succeeded by one in which they undergo gradual diminution. The diminution in rotation causes the upper surfaces of the laminæ nocturnally once more to be directed more and more forwards, reverting as they do so to a position more or less like that proper to an earlier stage of development. The reversion, however, is not complete, as it is interfered with by the coincident diminution in convergence and depression. Finally, a period arrives at which the progressive diminution leads to a complete abolition of all appreciable movement, and the pinnæ remain permanently fixed in what was previously the diurnal position, with the upper surfaces of their laminæ looking directly upwards in the plane of the rachis or slightly ascending from it, and their midribs at right angles to it, or even somewhat inclined backwards towards the base of the leaf.

On examining the secondary petiole of a pinna at the period at which movements are at their maximum, two distinct masses of pulvinar tissue may be recognised in it. They differ from one another in tint, the one having an ochreous tinge, whilst the other is pure green, and they are arranged in a peculiar spiral fashion (Plate III, Fig. 2, 3). The ochreous tissue at the base of the pulvinus lies antero-external, and farther out it becomes purely external; whilst the green tissue basally is purely axillary, but towards the laminar extremity invades the anterior surface of the pulvinus so as to become continuous with the mass of green parenchyma which forms a ridge over the course of the midrib. The pulvinus extends for some distance into the base of the lamina on the under-surface, and the green tissue on the inner side of the midrib is more conspicuous in amount than the ochreous tissue on the other side.

It is this spiral disposition of the opposed masses of pulvinar parenchyma that determines the peculiar character of the movements of the pinnæ. When the development of the pulvinus first begins, the fact that the tissue, which is subsequently distinguished by its ochreous tint, makes its appearance first accounts for the permanent depression and convergence of the pinna which prevails immediately antecedent to the period at which

movements first begin to appear The depression is determined by the accumulation of parenchyma over the anterior aspect of the base of the secondary petiole, and convergence by the extension of it along the course of the outer side When pulvinar parenchyma begins to accumulate beneath the base and along the axillary surface of the secondary petiole, and to extend thence over the anterior surface of the base of the lamina and outwards along the groove which originally corresponds with the course of the midrib, it tends more and more to cause elevation and divergence of the secondary petiole and expansion of the lamina, and when the tissue has attained sufficient structural power to resist the older masses of tissue making for depression and convergence of the secondary petiole and folding upwards of the halves of the lamina, a condition of permanent equilibrium is once more established Until this has occurred, however, movements necessarily continue to take place, because the fluctuations in turgescence which accompany the presence or absence of solar stimulation in the younger and more recently developed masses of tissue are greater than those taking place in the older ones So long as this is the case, the younger tissue is relatively stronger during the day than it is at night, and consequently it is able to effect displacements diurnally which it is incapable of maintaining nocturnally The magnitude of the movements goes on steadily increasing so long as the differences between the functional and structural strengths of opposed masses continue to increase, but, when the development of the older mass has once been completed, the movements diminish with the continued development of the younger mass, and they ultimately disappear when the tissue in it has overtaken that of its opponent in respect to structural strength and functional weakness At the outset the tissue which makes for the diurnal position is present in very small amount as compared with that which makes for the nocturnal one, and consequently the amount of displacement which it is able to effect is very limited Subsequently it increases rapidly in bulk, but at the same time the permanent structural power of its opponent has also undergone increase The mass of functionally stronger tissue increases, but the strength of the structurally stronger one does so also up to a certain point The increased bulk of the functionally stronger tissue enables it to give rise to increased displacement under the influence of solar stimulation, but so long as the differences in permanent structural strength of the two masses go on increasing, the amount of resistance which the structurally stronger one is capable of overcoming in the absence of solar stimulation will undergo increase also In consequence of this we find that nocturnal displacement does not attain its maximum in pinnæ which have just begun to move but goes on steadily increasing for a considerable time. The precise amount of movement exhibited by any particular pinna at a given period in the course of its development depends not merely on the relative bulks of the opposing masses of pulvinar tissue, but on the differences which they present in regard to functional and structural strength The amount of diurnal displacement is at first small owing to the small bulk of the tissue giving rise to it, and the nocturnal displacement does not attain its maximum at first, because the mass of tissue which determines it goes on for some time increasing in structural strength in relation to its opponent Just before the primary initiation of movement in a pinna the supero external mass of pulvinar parenchyma is already conspicuous, whilst its opponent is practically absent in a mature or motionless pinna this condition is more or less reversed, the mass of the axillary tissue being somewhat in excess of that of the external one Owing to the fact that all the pinnæ in a leaf are not matured simultaneously, but progressively from the base to the

apex of the rachis, the diurnal and nocturnal positions of all the individual pinnæ in one and the same leaf are not uniform during the greater part of the period during which appreciable movements are present. This is clearly illustrated by the following notes regarding the nocturnal positions of the pinnæ in a single leaf. All of the pinnæ were closely convergent to the line of the petiole and depressed beneath it. In the two terminal pairs depression was not so great as in the succeeding ones, and the halves of the lamina were somewhat folded upwards. In the next four pairs depression and convergence were extreme, and the laminæ were fully expanded, and had their upper surfaces facing directly forwards to the tip of the leaf. In the next pair the upper surfaces of the laminæ were slightly inclined inwards, and in the succeeding three pairs they faced almost directly inwards. In the two basal pairs depression and rotation were already somewhat diminished, and the upper surfaces of the laminæ were consequently directed forwards, upwards, and inwards. In this leaf the distal pairs of pinnæ had not yet attained to the maximum of movement, whilst the basal ones had already begun to decline from it.

The phenomena of movement in the leaves of *Cassia Sumatrana* indicate just as clearly as those of *Cassia alata* that they correspond with the interposition of a period of instability between two periods of stable equilibrium in the tissues of the motor organs, and that, so long as movements continue to occur, the assumption of the nocturnal position is always owing to the action of a tendency to the resumption of what was either the primary permanent position or the diurnal position at an earlier stage in the evolution of the pinnæ. In the initial periods of movement, the nocturnal convergence, depression and elevation of the halves of the lamina give rise to complete reversion to the antecedent permanent position. Somewhat later rotation comes in to interfere with the completeness of the reversion and to replace folding of the lamina. So long as folding is possible, the action of the portion of the mass of pulvinar parenchyma making for the noctural position, which is prolonged into the under surface of the lamina, assists in elevating the outer half of the lamina from the plane of the midrib; but when permanent expansion has been established, folding is no longer possible, and the same action tends to cause torsion of the midrib. Rotation is, however, a comparatively transitory phenomenon here as compared with the rotation of the pinnæ of *Cassia alata*, because there is no excessive accumulation of pulvinar parenchyma on the under surface of the outer half of the lamina, so that the growth of the opposing tissue on the other side of the pulvinus comparatively rapidly provides sufficient resistance to prevent the occurrence of torsion of the midrib and vascular axis of the pulvinus. Rotation is thus present only during the period at which the mass of pulvinar tissue making for the noctural position possesses its maximal relative strength.

In *Cassia Sumatrana*, as in *Cassia alata*, the movements of the leaves, although of very considerable magnitude when at their maximum, are invariably slow and gradual. In both cases the tissues of the motor organs do not provide any special filtrative facilities, either in the form of abundant pitting of the cell-walls or of an extensive system of intercellular spaces (Plate VII, Fig. 2), and hence any factors which tend to give rise to sudden increments in external pressure or to sudden increase in general loss or decrease in general supply of fluid, are incapable of producing any immediately appeciable effects on turgescence.

CHAPTER IX.

The movements of the leaves of Pithecolobium Saman and Leucaena glauca.

The movements of the leaves of *Pithecolobium saman* are distinguished from those occurring in the leaves of either of the species of *Cassia* which have been treated of in the previous pages by much greater persistence and by the relative rapidity with which they are executed The movements of the primary petioles, although originally very conspicuous, do undergo rapid diminution at a comparatively early period in the life of the leaves, and are practically absent latterly, but those of the secondary petioles and pinnules are very much more persistent, and it is only in very old leaves that they become inconspicuous When the movements are at a maximum, the diurnal and nocturnal positions are of the following nature —diurnally, the primary petiole and rachis are very widely divergent from the axis, lying almost at right angles to it, the secondary petioles and rachises are also very widely divergent from and lie almost in the same horizontal plane as the primary ones, and the pinnules are in the same plane and have their midribs diverging from the line of the secondary rachises at angles of rather more than 45 degrees Nocturnally, the primary petiole is so highly convergent that it not unfrequently actually crosses the line of the axis, the secondary petioles are converged and so deeply depressed that they come to point more or less backward towards the base of the leaf (Plate VII, Fig 7), the pinnules are folded almost directly upwards, so that the upper surfaces of those of the opposite sides of the secondary rachises are in close contact, their midribs being directed upwards and forwards at vertical angles with the line of the secondary rachises of almost the same degree of inclination as that of the diurnal horizontal one, in other words, they have undergone almost pure elevation apart from any appreciable rotation

When dealing with the subject of nyctitropic movements generally, it has already been pointed out that the nocturnal position in this case is specially clearly one of reversion to what was the permanent one at a period immediately preceding the time at which periodic movements first begin to make their appearance, and that the diurnal divergence of the primary petiole is essentially connected with the gradual development of a great mass of axillary pulvinar parenchyma The action of the diurnal rise in turgescence in the primary pulvinus must, however, in this case be greatly aided in effecting divergence by the coincident increase in turgescence and alteration in the position of the distal portions of the leaf, which imply corresponding increase in distal leverage The leverage here aids in establishing the diurnal position, and renders it more stable than it would otherwise be, or than it is in leaves like those of *Mimosa pudica*, in which distal leverage opposes, in place of aiding, the tissue in the primary pulvinus which makes for the diurnal position, and to it, no doubt, to a great extent is due the phenomenon of rapid diminution and early disappearance of movement in the primary petiole Large leaves are provided with from six to eight secondary rachises which bear from three to eight or nine pairs of pinnules, the number of the latter being smallest in the basal rachises and increasing progressively towards

the distal portions of the leaf. In the case of five large leaves in which the actual number of secondary rachises and pinnules was counted, that of the former varied from twelve to sixteen, and that of the latter from seventy-eight to one hundred and four, which very conclusively indicates that the amount of leverage telling on the primary pulvinus in favour of divergence must be very considerable; and so considerable is it that, in co-operation with the great progressive development of the mass of axillary parenchyma (Plate I, Fig. 14), it not unfrequently leads to the leaf ultimately becoming permanently directed more or less backwards towards the base of the axis. In the case of the primary petiole and rachis there is a nocturnal reversion to a previously permanent position, only slightly modified by a certain amount of increase in convergence; but in that of the secondary ones considerable modification is present owing to the fact that for some time the amount of nocturnal depression goes on steadily and progressively increasing. The nocturnal position of the pinnules, on the other hand, is one of pure reversion, and the alternate movements of diurnal depression and nocturnal elevation which they undergo are the exact parallels to the alternate unfolding and folding of the laminæ of young pinnæ of the species of *Cassia*. There is no appreciable rotation similar to that occurring in the case of these pinnæ, because the opposing masses of pulvinar tissue making respectively for the diurnal and nocturnal positions lie directly superior and inferior, and are related to the upper and under surfaces of both halves of the lamina alike. The inferiorly situated mass of parenchyma is aided in giving rise to nocturnal elevation of the pinnule by the action of the vascular axis of the pulvinus, which constantly tends to resume its original direction to the secondary petiole. It is thus only after it has attained considerable magnitude that the superior mass of pulvinar parenchyma is able to overcome the resistance of the inferior one and of the vascular bundle; and, even when it has attained its maximum development, it is, as a rule, incapable of securing complete depression of the pinnule to the plane of the secondary petiole. The great relative increase in bulk of the superior mass of pulvinar parenchyma as compared with the inferior one, which takes place during maturation of the leaf, is illustrated in Figs. 16 and 17 of Plate I.

The opposed masses of parenchyma in the secondary pulvini are essentially disposed altogether superiorly and inferiorly; but yet the movements which actually occur are not movements of simple depression and elevation, but of depression and convergence, and of elevation and divergence. This is owing to the peculiar relation which the pulvini bear to the bevelled petiolar surfaces with which they are connected (Plate IV, Fig. 5). The superior mass of pulvinar parenchyma, as the figure shows, is so situated as to lie so much above the level of the bevelled surface of the primary rachis that any alterations in its relative strength and pressure can only act appreciably in giving rise to movements of elevation and depression; but in the inferior pad, which is internally in close contact with the bevelled surface, any increase in its turgescence must tend not merely to give rise to elevation, but also to divergence of the secondary petiole. In the normal passive position, as determined by purely structural features, the axial vascular bundle of the secondary pulvinus lies almost parallel with the line of the primary petiole; and any rise in turgescence in the axillary portion of the inferior mass of pulvinar parenchyma must tend to cause divergence, owing to the relation which the tissues of the rachis and pulvinus bear to one another. The movements are not in this case complicated by the presence of any

rotation like that which occurs in those of the secondary pulvini of the *Cassia*, because they are not related to the presence of any structural arrangements corresponding to the laminar expansions of pulvinar tissue, which are present in the latter

It is the very peculiar form of the vascular axis in the secondary pulvini that is the principal determinant of the extreme convergence and depression of the secondary petioles during the night (Plate IV, Figs 4 5) The vascular tissue, in place of forming a more or less rounded cord, as it does in the case of the secondary pulvini of *Mimosa pudica*, or a tube filled with medulla as it does in those of *Leucæna glauca*, takes the form of a broad, flattened, slightly curved band This naturally implies corresponding modification in the resistance which it will present to horizontal and vertical displacement from its normal passive position It is morphologically adapted to afford very considerable resistance to the divergence which is determined by the axillary portion of the inferior mass of pulvinar parenchyma, and consequently, when the latter loses turgescence with the removal of solar stimulation, it acts powerfully in producing convergence But its resistance to depression is very feeble, and the distal leverage to which it is exposed is very great—the pulvinus only weighs from 4 to 7 per cent of the entire secondary petiole and pinnules —and consequently when it loses the support afforded to it by the diurnal excess of turgescence in the inferior mass of pulvinar parenchyma, it yields to the leverage aided by the action of the relatively feeble superior pulvinar parenchyma The central portion of the inferior pulvinar pad is not only thicker, but also much richer in chlorophyll, than that of the superior one is, and consequently, when in a condition of diurnal turgescence, it is able not only to overcome it, but to overcome the action of distal leverage on the vertically flexible vascular axis of the pulvinus The lateral portions are not conspicuously thicker than those of the superior pad, but the inner of them, when in a condition of diurnal turgescence is, from its axillary position, enabled to effect divergent displacement of the vascular bundle in spite of the relatively great resistance which it opposes to horizontal flexion (Plate IV, Fig 5)

In the secondary and specially in the tertiary pulvini, during the period in the life of the leaf in which extensive movements are regularly carried out, the masses of tissue which make for the diurnal position are conspicuously distinguished by their colour from those which make for the nocturnal one In both cases they are of a deep green, whilst their opponents have a much paler ochreous green tinge (Plate IV, Figs 3, 5—9) Consequently, in the case of the secondary pulvini, it is the inferior mass of parenchyma which is green and the superior which is ochreous, whilst in the tertiary ones precisely the reverse holds good

The opposed masses of parenchyma in the primary pulvini do not show such conspicuous and readily appreciable differences in colour as the corresponding tissues in the secondary and tertiary pulvini do, but the steady and progressive increase in relative bulk which takes place in the superior one coincidently with diminution in and final abolition of the assumption of the nocturnal position by the primary petiole is very striking (*Vide* Plate I, Figs 14, 15, Plate IV, Figs 1, 2) In leaves in which petiolar movements are at a maximum, the superior mass is distinguished merely by the fact that it is vivid green almost throughout its entire thickness Whilst, in the inferior mass, the tissue nearest the wood is almost colourless, and the superficial band of green has a somewhat olive tinge Microscopic examination, however, shows that the tissue of the superior mass is composed of cells which are of considerably smaller size and much more richly provided with green chromatophores than those

of the inferior one are. There is thus ample provision for a relative excess of diurnal turgescence in it, and this, in co-operation with the diurnal rise in leverage in the distal parts of the leaf accompanying solar stimulation, is quite sufficient to account for the occurrence of diurnal divergence. The inferior mass shows no distinct evidence of any considerable excess in relative structural strength; but it is aided in its tendency to give rise to convergence by the strength of the axial mass of wood and medullary tissue, and consequently nocturnal convergence is for a time extreme. The wood apparently plays a much more important part here in determining the assumption of the nocturnal position than it does in the case of the secondary and tertiary pulvini. The struggle in the primary pulvini is, to a great extent, not so much between the opposed masses of pulvinar parenchyma, as between the superior mass which tends to cause divergence and the wood which makes for convergence in the effort to regain its original direction in relation to the axis. For a time the nocturnal loss in turgescence in the superior mass of pulvinar parenchyma, and the coincident diminution in leverage of the distal portions of the leaf, allow the strong woody tissue to resume its original direction to the axis, and even to pass beyond it owing to the adjuvant action of the inferior parenchyma; but the movement rapidly diminishes and ultimately disappears with the continued increase in bulk and structural strength of the superior parenchyma, leaving the primary petiole in a permanent position of extreme divergence or even more or less inclined backwards from the line of the axis. So long as the movements continue to occur, they lead very conspicuously to that assumption of the maximal nocturnal position during the earlier part of the night, followed by gradual departure from it in spite of continued absence of solar stimulation, which, as has already been pointed out, is so characteristic of nyctitropic movements generally.

The pulvinar tissues in *Pithecolobium* are relatively dense (the system of intercellular spaces being comparatively limited), but pitting of the cell-walls is very much more conspicuous and abundant than it is in the pulvini of either of the species of *Cassia* (Plate VII, Figs. 3, 8), and with this we find a capacity for much more rapid movements in the leaves. At a period in the evening at which leaves of the species of *Cassia* are only beginning to show indications of departure from the diurnal position, those of *Pithecolobium saman* are already in the fully developed nocturnal one. This may be partially due to the greater facilities for active transpiration which they present in connection with their great excess in stomata; but the fact that similar phenomena present themselves in connection with continued agitation by showers of violent rain indicates that it is mainly determined by textural facilities for redistribution of liquid. An amount of agitation by wind or tropical showers which hardly produces any appreciable effects on *Cassia alata*, suffices to produce maximal movement in the secondary petioles and pinnules of *Pithecolobium*. The total amount of displacement involved in the transition from the diurnal to the nocturnal position in both cases alike is very great; but the rate at which it can be effected is very different owing to the presence of structural peculiarities, which in the case of *Pithecolobium* are of a nature to permit of redistribution of fluid by filtrative discharge from the cell-cavities of the pulvinar parenchyma taking place much more rapidly than is possible in the case of either of the species of *Cassia*.

In so far as strictly nyctitropic movements—movements dependent on fluctuations in turgescence, determined by variations in degree of solar stimulation,—are concerned, another factor, however, comes into play besides the mere structural facilities for the escape of fluid from the cell cavities of the motor organs, and for transpiratory loss

from the tissues generally There can be no question that the pulvinar tissues in *Mimosa pudica* provide much greater facilities for filtrative redistribution of fluid than those of *Pithecolobium saman* do, and that the laminæ contain an excess of stomata, and with this we find a corresponding increase in capacity for rapid movement in connection with the incidence of mechanical agencies favouring increased local filtration owing to increased pressure But yet the assumption of the nocturnal position occurs later under normal conditions in *Mimosa* than in *Pithecolobium.* The only explanation for this apparent anomaly must lie either in differences in the stability of the osmotic pro ducts which are formed under the influence of solar stimulation of the tissues, or in differences in the degree of protoplasmic stimulation and activity attending particular degrees of illumination in the two cases, and as we find that the leaves of *Mimosa* not only assume the nocturnal position later, but resume the diurnal one earlier, than those of *Pithecolobium* do, and that when once they have begun to show movements in either direction the latter are executed with relatively great rapidity, there can be little doubt that the second explanation is the correct one The activity of the pro toplasts in *Mimosa* must apparently be fully called into play and maintained by degrees of illumination which are incapable of producing an equally stimulant action on those of *Pithecolobium*

In *Leucœna glauca* the movements in the secondary rachises and pinnules present a general resemblance to those occurring in the corresponding parts of the leaves of *Pithecolobium saman*, but from the outset the primary petioles, although provided with a most conspicuous pulvinus, fail to exhibit any appreciable periodic movements and in place of these show steadily progressive divergence and rotation The absence of periodic movements *is no doubt partially, at all events, connected with the fact that* the primary petiole is considerably weaker in relation to the other parts of the leaf than it is in the case of *Pithecolobium* In the latter the primary petiole contributes about 20 per cent to the total weight of the leaf, whilst in *Leucœna* it contributes only half as much, and, as this difference coincides with corresponding differences in the strength of the vascular axis of the primary pulvinus, it is evident that in *Leucœna* the action of the latter as a factor making for convergence in consequence of its tendency to resume its original convergent position in relation to the axis will be proportionately feeble The leaves are ordinarily provided with from four to seven secondary *rachises*, each of which bears from nine to fifteen pairs of narrow pinnules which are set on at comparatively wide intervals, so that, when the leaf is in a con dition of full expansion, each of them is completely isolated from its neighbours and there is an absence of any overlapping of successive pairs like that which is ordinarily present in the leaves of *Mimosa pudica* under similar circumstances

Owing to the very lax habit of the plant, the growing portions of the shoots are almost invariably more or less horizontally disposed, and it is in connection with this that a necessity for excessive rotation of the primary petioles has arisen Rotation does present itself in the case of certain leaves of *Pithecolobium saman*, but the phenomenon is not of constant occurrence as it is in *Leucœna glauca*, and its predominance in the latter is owing to the horizontal disposition of the axis on which the growing leaves are situated The mature leaflets are practically arranged in two rows, one lying on either side of the axis, and with their surfaces facing directly upwards in the same direction as the upper surface of the axis This position, however, necessarily implies the antecedent occurrence of a varying, and in most cases excessive

amount of rotation, seeing that at an early stage of development the upper surface of the primary rachis faces directly inwards to the axis, just as it does in the case of *Pithecolobium saman.* Where the growing shoots are either erect or more or less ascending, as they are in *Pithecolobium saman,* simple divergence, or divergence accompanied by a limited amount of rotation of the primary petiole, will suffice to cause the upper surfaces of the primary rachises to face directly upwards; but where the axis is more or less horizontal, it is clear that simple divergence could only produce such an effect in the case of petioles which originally faced directly downwards, and then only when carried out in very excessive degree, and that in all other cases rotation (and frequently excessive rotation) must necessarily come into play. The ultimate position of the leaves is not, however, entirely due to rotation of the petioles, but also to the occurrence of a certain amount of spiral movement in the growing axis, which in the course of development undergoes a sort of uncoiling, so that each successive leaf at a certain period comes to be more or less laterally situated. A mass of pulvinar parenchyma is gradually developed over the outer face of the base of the petiole. The accumulation of tissue is not, however, uniformly distributed, but predominates on that side which is for the time being the inferior one; and, with this, rotation of the petiole gradually sets in and advances through a quadrant, so that the originally inferior aspect comes to be axillary, and its structurally axillary one comes to look directly upwards. But, owing to this rotation, the predominant mass of pulvinar parenchyma which was originally inferior necessarily assumes an axillary position, and consequently makes for divergence in place of lateral elevation of the petiole. In the mature leaves a great mass of axillary pulvinar parenchyma is very conspicuous; this, however, does not belong to the structurally axillary face of the petiole, but to that lateral aspect of it which originally was directed downwards. The extreme inequality in the development of pulvinar tissue in respect to the two sides of the vascular axis of the pulvinus, together with the weakness of the latter, is illustrated in Plate III, Figs. 5, 6.

Whilst periodic movements are relatively inconspicuous in the primary petioles, they are highly developed and very persistent in the case of the secondary rachises and pinnules. As in other instances, they are primarily absent; but from the time at which they appear, they normally continue to be carried out with unimpaired vigour during the entire period in which the leaves retain a healthy character. In this respect the leaves resemble those of *Mimosa pudica* much more closely than do any of the leaves which have hitherto been considered. Before the period at which periodic movements set in, the secondary petioles are primarily directed upwards and forwards from the line of the primary one, and are so closely convergent as to have their inner surfaces in contact with one another (Plate III, Fig. 7). Somewhat later they become somewhat divergent whilst still retaining their ascending direction (Plate III, Fig. 7). Both divergence and elevation next undergo progressive diminution; and, immediately prior to the onset of periodic movements, the secondary petioles are once more closely convergent to the line of the primary one, and lie in the same plane with it or slope slightly downwards from it. When periodic movements do make their appearance, they give rise to alternating nocturnal convergence and depression and diurnal divergence and elevation to the plane of the petiole. The pinnules, like those of *Pithecolobium saman* and *Mimosa pudica,* are from the outset fully expanded and, until the onset of periodic movements, are directed forwards in a line parallel with that of the

secondary petiole, with the upper surfaces of those of the opposite rows in close contact with one another, and their surfaces facing directly outwards, the outer or posterior half of the laminæ lying vertically over the axillary half, and the midrib pointing directly forwards. When movements set in they lead to progressively increasing diurnal divergence, rotation and depression of the laminæ which ultimately come to lie in the same plane with the upper surface of the secondary petiole, and more or less at right angles to it, with their upper surfaces facing directly upwards alternating with a nocturnal resumption of the originally permanent position, or rather of that position slightly modified by the fact that the midribs now, as a rule, no longer point directly forwards, but slightly downwards from the line of the secondary petiole. The movements of the pinnules thus differ from those in the pinnules of *Pithecolobium saman*, and are of the same nature as those in the pinnæ of *Cassia alata* in consisting not merely of alternating elevation and depression, but of alternating elevation and depression combined with a considerable amount of rotation.

The structural features which determine the character of the movements of the secondary petioles are of the following nature. When an accumulation of pulvinar parenchyma begins to be developed, it appears first over the upper half of the base of the secondary petiole, and, together with the increasing leverage of the distal parts, tends to give rise to gradual depression. At a somewhat later period accumulation begins over the lower half, and thus of course makes directly for elevation. In mature but still freely motile pulvini, there is little difference in the thickness of the cell walls in the various portions of the parenchyma, but the mass which lies to the axillary side of the axis is distinguished from the outer one by greater thickness (Plate III, Fig. 9), and by containing a greater number of green chromatophores. It is this, together with the fact that the axillary masses on undergoing any increase in turgescence press upon the resistent rachis in the case of all the pinnæ but the terminal ones, and against one another in the latter, that determines the great diurnal divergence of the secondary petioles. The external mass of pulvinar parenchyma is less bulky and poorer in chlorophyll, and consequently undergoes less increase in turgescence diurnally than its opponent, and moreover, it is related basally to a mass of spongy tissue very poor in chlorophyll content (Plate III, Fig. 9) so that any rise in turgescence which it does undergo is in great measure expended in compressing this feeble tissue. With the absence of any conspicuous structural differences between the superior and inferior parenchyma, and the presence of a relatively strong vascular axis (Plate III, Figs. 8, 9) which presents very considerable resistance to both vertical and horizontal flexion, we find the amount of vertical movements becoming very inconsiderable. In *Pithecolobium* the secondary rachises in leaves at the stage in which movements are at a maximum are nocturnally directed backwards at acute angles to the line of the primary one, but in *Leucæna* they never attain to a right angle to it, but are invariably directed forwards at very acute angles towards its apex. The really important struggle is that which is carried on between the strong vascular axis of the pulvinus and the mass of parenchyma lying to its axillary side, and which is diurnally able to divert it from its normal passive direction. The axillary parenchyma, from its position, its greater bulk, and its greater richness in chlorophyll, is able not only to do away with any effects of diurnal rise in turgescence in the external pad, but also to cause extreme divergence of the resistent vascular axis. In the case of highly developed pulvini the vascular axis is reduced to the form of a solid cord containing no medullary tissue. When this has a cylindrical form, as in the

secondary pulvini of *Mimosa pudica*, the masses of pulvinar parenchyma surrounding it either equal or exceed it in thickness; whereas in the secondary pulvini of *Pithecolobium saman* it takes the form of a flattened band, the superior and inferior masses exceed it in vertical diameter, and the lateral ones falling short of it in horizontal diameter; but in the secondary pulvini of *Leucæna glauca* the thickness of the axial mass of vascular and medullary tissue considerably exceeds that of the surrounding masses of pulvinar parenchyma in every direction. (Plate III, Figs. 8, 9.)

In the case of the tertiary pulvini the opposing masses of pulvinar parenchyma are disposed above and beneath the vascular axis, but the movements which they determine are not simple movements of depression and elevation, like those present in the pinnules of *Pithecolobium saman*. This is owing to the following facts. In the first place, the pulvini are obliquely set on upon a bevelled surface, so that the opposed masses are directed respectively upwards and forwards and downwards and backwards, just as they are in the tertiary pulvini of *Mimosa pudica* (Plate V, Fig. 5); and in the second place, they hold a relation to the lamina of the pinnule very similar to that which is present in the case of the pinnæ of *Cassia alata*. The oblique disposition of the opposing pulvinar masses necessarily implies that the upper one must make not merely for depression, but also for backward displacement of the lamina, and the under one not merely for elevation, but for elevation and advance. So far, of course, we are dealing with movements of depression and elevation on an oblique surface, but the character of the movement is further modified by the unlike relation which the masses of pulvinar parenchyma bear to the two halves of the lamina. There are conspicuous expansions of pulvinar tissue involving the base of the posterior or outer half of the lamina both on its superior and inferior aspects (Plate III, Fig. 10), and these, of course, must tend respectively to determine rotation outwards and inwards of the upper surface of the midrib according to the variations in their relative strength and resistance. The inferior pulvinar pad consequently not only makes for general advance and elevation of the lamina, but for excessive elevation of its outer half, and when once the displacement has advanced so far that the posterior side of the keel of the midrib comes to lie superior to the anterior side, to a deflection of the pinnule. The ultimate outcome of the conditions is that when the leaf is in the fully developed nocturnal position, the pinnules not only have their upper surfaces facing directly inwards, but slope downwards and forwards from the plane of the petiole. An increase in the relative strength of the upper mass of pulvinar parenchyma conversely not only gives rise to depressive divergence and retrocession, but also to special depression of the outer half of the lamina, and consequently to rotation of the vascular axis, so that the upper surface of the midrib, in place of facing inwards, faces directly upwards, and the upper surface of the lamina lies in the same plane with and more or less at right angles to the secondary rachis. There is not any very conspicuous difference in the strength and thickness of the cell-walls of the opposing masses of tissue, but the superior one is considerably richer in chlorophyll corpuscles than the inferior one is.

The pulvinar tissues in *Leucæna glauca* are even more extensively and conspicuously pitted than those of *Pithecolobium saman* are: but they resemble the latter, and differ from those of the primary pulvini of *Mimosa pudica*, in being throughout devoid of any highly developed system of intercellular spaces (Plate VII, Figs. 3, 4, 5). This is specially conspicuous in regard to the primary pulvini of the deeper strata which in *Mimosa pudica* are not merely very extensively pitted, but are of extremely

open texture, whilst in *Pithecolobium* and *Leucæna* they contained merely minute angular intercellular spaces like those of the superficial ones Corresponding with these differences in the degree to which facilities for redistribution of fluid are present, we find differences in regard to the rate at which movements are executed The leaves of *Leucæna* move more rapidly than those of *Pithecolobium*, but not nearly so rapidly as those of *Mimosa* When the temperature is high and atmospheric humidity low, a certain amount of depression of the secondary rachises and convergent elevation of the pinnules makes its appearance almost immediately after a leaf or shoot has been detached from the axis, and much sooner than any corresponding displacements are visible in leaves of *Pithecolobium* exposed to similar conditions This is in one respect remarkable as the numbers of stomata in *Leucæna* are very much smaller than in *Pithecolobium* In spite of this, however, transpiratory loss takes place with very great rapidity, probably in connection with the general delicacy of the tissues, as is indicated unequivocably by the very early onset of phenomena of general wilting As the atmospheric humidity rises, the rate of movement falls, and when a condition approaching saturation is present, movements are very greatly retarded so long as mechanical disturbances of the leaves calculated to give rise to increased filtrative discharge of fluid from the pulvinar tissues are absent In *Leucæna* movements tending towards the establishment of the nocturnal position may, even more distinctly than in the case of any of the leaves which have been previously described, be recognised as arising under the influence of many different conditions which only agree with one another in the fact that they all tend to induce diminished turgescence in the pulvinar tissues In cases of separation of leaves or shoots from the axis, diminished turgescence arises in consequence of arrested supply and continued transpiratory loss of fluid, where movements occur in connection with continued exposure to hot dry air without separation from the axis, excess in transpiratory loss acts alone, where they follow much mechanical agitation, increased local filtration in the pulvinar tissues comes into play, and, finally, where they attend removal of solar stimulation, a fall in osmotic capacity of the cell sap is the determinant In all cases alike, the loss of strength, or, in other words, the diminution in turgescence falls most heavily upon the younger and functionally most active masses of tissue, and consequently, in all alike, the movement which attends it is in the direction of the position which is made for by the older masses of pulvinar tissues, because they are the structurally stronger and functionally weaker ones In certain cases the struggle is mainly between opposing masses of pulvinar parenchyma, whilst the vascular tissues are practically passive, in others the vascular tissues co operate with the older masses of pulvinar parenchyma, and in still others they become the main determinants of the assumption of the nocturnal position In any case, however, the struggle is between functionally powerful and structurally powerful tissues, the former constantly making for the diurnal and the latter for the nocturnal position The tissues which are distinguished by structural strength neither undergo so much diurnal increase in turgescence nor provide such facilities for filtrative loss of fluid, as those which are characterised by excess in functional strength, and consequently they are not subject to so much loss of turgescence on removal of solar stimulation or on the incidence of conditions calculated to give rise to increased filtration as the latter are, so that any deprivation of light or increase in pressure on the pulvinar tissues must tend to give rise to an assumption of the nocturnal position When we compare the rates at which movements

are executed by the leaves of various species of plants, we find that a distinct and direct relation is traceable between rapidity of movement and textural facilities for filtration. In the case of *Cassia a'ata* and *C. sumatrana*, the movements, when at their maximum, are very extensive, but are invariably slowly and gradually carried out, and the pulvinar parenchyma is very dense and scantily pitted; in *Pithecolobium saman*, and even more in *Leucæna glauca*, the rate of movement is considerably increased, and the pulvinar parenchyma, although unprovided with a fully-developed system of intercellular spaces, is composed of cells the walls of which are very abundantly pitted; and in the primary pulvini of *Mimosa pudica* movements attain a maximum rapidity, and the tissues are not only most elaborately and extensively pitted, but are provided with a very highly-developed system of intercellular spaces, affording abundant accommodation to any fluid which may escape from the cell cavities in consequence of any increased filtration.

CHAPTER X.

The movements of the Leaves of Mimosa pudica.

The general appearance of the leaves of *Mimosa pudica* is, of course, familar to every one, but it is necessary to allude to certain of their characters in somewhat detailed fashion, seeing that these have an important bearing on the rapidity with which they are capable of executing movements under certain conditions.

The following data were obtained from a single, large, active leaf:—

1.	Weight of the entire leaf	0·56 grammes.
2.	Weight of the petiole including the primary pulvinus ...	0·06 "
3.	Weight of the secondary pulvini, secondary petioles and pinnules	0·50 "
4.	Length of primary pulvinus	0·23″ "
5.	Thickness of primary pulvinus	0·065″ "
6.	Length of primary petiole from the distal extremity of the primary pulvinus to the points of origin of the proximal pairs of secondary ones	1·92″ "
7.	Length of the remaining portion of the primary petiole between the sites of origin of the proximal and distal pairs of secondary pulvini	0·125″ "
8.	Length of the secondary petioles, including the secondary pulvini—	
	(*a*) Proximal pair	2·20″ "
	(*b*) Distal pair	2·92″ "
9.	Length of secondary pulvini	0·12″ "
10.	Thickness of secondary pulvini	0·09″ "
11.	Number of pinnules on secondary petioles—	
	(*a*) Proximal pair	19, 19
	(*b*) Distal pair	25, 24
12.	Area of laminar surface (determined by gumming down the detached pinnules on a sheet of paper, so as to form a continuous stratum)	7 square inches.
13.	Number of stomata—	
	(*a*) Superior epidermis	160,000 per square inch.
	(*b*) Inferior epidermis	400,000 "
14.	Number of stomata on entire laminar surface	3,920,000

In the case of another leaf, of which careful weightments were made, the results were as follow —

1	Weight of entire leaf	0 47 grammes
2	Weight of primary petiole including primary pulvinus	0 07 ,,
3	Weight of primary pulvinus	0 01 ,,
4	Weight of secondary pulvini, secondary petioles and pinnules	0 40 ,,
5	Weight of primary petiole without the primary pulvinus	0 06 ,,

The most important points to be noted are, *first*, the great leverage to which the primary pulvinus is exposed (*vide* Appendix A) and, *second*, the excessive transpiratory facilities which are provided by the laminar surfaces Taking the data derived from the second leaf in which the weight of the primary pulvinus was determined, it appears that the pulvinus had to support a weight forty six times as great as its own, and of which 85 per cent was situated at the distal extremity of an elongated rigid lever, represented by the primary petiole The power in this lever system is applied at the immediate neighbourhood of the fulcrum, and the weight is situated at the end of a long lever—conditions implying extreme instability of equilibrium in event of any fluctuations in the power The excess of transpiratory facilities furnished by the laminar surfaces is mainly due to the fact that both the inferior and superior epidermis are provided with stomata (Plate V, Figs 9, 10) The numbers of stomata on the inferior epidermis are not in excess but rather fall short, of those present on the inferior surface of the pinnules of *Pithecolobium saman*, but in the latter, as well as in the other nyctitropic leaves which have been specially considered here, the superior epidermis is entirely wanting in them Additional facilities for the occurrence of active transpiratory loss are, moreover, provided by the extremely open character of the parenchyma intervening between the pallisade cells and the inferior epidermis (Plate V, Fig 11) There are thus structural grounds for assuming that very active transpiratory loss of fluid must occur under favourable circumstances, and that such loss actually takes place is demonstrated by the following experimental data —

Experiment I—A pot plant of *Mimosa pudica* bearing seven leaves was taken The hole in the bottom of the pot was firmly corked, and the entire outer surface and lip were thickly coated with melted wax A glass plate, large enough to cover the mouth, was then divided into two halves, and a small piece was filed out in the centre line of division, so that when the halves were adjusted to one another they formed a plate with a small central perforation These were next luted down with melted wax over the mouth of the pot, so that the lower part of the axis of the plant passed through the central opening and, finally, the line of division and the opening were also carefully luted The pot was next placed in an hermetically closed chamber containing a vessel the weight of which had been determined, and which contained 50 grammes of pure sulphuric acid, and the whole apparatus was set in the open air in diffused sunlight The leaves remained in a state of extreme expansion and elevation At the close of four hours the sulphuric acid was removed and weighed, and the weight amounted to 51 6 grammes, indicating an absorption of 1 6 grammes of water of transpiration The acid was now returned to the chamber, and the latter anew hermetically sealed, and on the following day it weighed 54 1 grammes, corresponding to an absorption of 4 1 c c of water during the period of twenty four hours The cover of the pot was now removed

and the earth gently washed away under a stream of running water, so as to free the roots without injury. The entire plant was next weighed, and the weight was ascertained to be only 2·03 grammes. A certain amount of the increment in weight which was sustained by the acid during the course of the experiment must, of course, be credited to the atmospheric humidity of the air of the chamber; but as the latter was a very small one, the mass of water furnished by transpiratory loss during twenty-four hours must have weighed nearly twice as much as the entire plant furnishing it.

Experiment II.—A plant with five leaves and weighing 2·32 grammes was treated in exactly the same fashion as that in the previous experiment. At the close of four hours' exposure the sulphuric acid indicated a gain of 1·5*c.c.* of water, equivalent to a mass of more than half the weight of the entire plant. (*Vide* Appendix B.)

The extreme activity of transpiratory loss is further very clearly indicated by the phenomena which attend exposure to direct sunlight. When the soil and air are dry continued exposure to the rays of the sun is followed by a complete assumption of the nocturnal position by the various parts of the leaves, and, even when soil and air are both comparatively humid, a very brief exposure to direct insolation is sufficient to give rise to various degrees of elevation of the pinnules. The phenomenon is particularly striking when it occurs in a large bed of the plant, a portion of which is artificially shaded, owing to the contrast presented by the fully expanded leaves within the limits of the shaded area and those in the insolated one. Taking the experimenta and natural data together, they appear very clearly to indicate that the diurnal position of the leaves is one of very unstable equilibrium dependent on a definite relation between supply and loss of water, and liable to be disturbed by any conditions implying either diminution in supply or increase in loss. The phenomenon of partial assumption of the nocturnal position by the pinnules under the influence of direct insolation, even where the humidity of the soil is very high, may be taken as indicating the existence of a definite limit to the activity of root absorption; but from experimental data, which will be furnished presently, it appears not unlikely that another factor comes into play to produce the result. The elevation of temperature which attends direct insolation not only gives rise to increased transpiratory loss, but must also cause an expansion of the gaseous contents of the water-conducting system which may well act as an obstruction to the passage of liquid along it; so that the departure from the diurnal position may be owing, not merely to increased transpiratory loss, but to diminished supply of water. That this is actually the case is certainly suggested by the fact that direct insolation, even within a closed moist chamber, is attended by a certain amount of elevation of the pinnules. Here, of course, the atmosphere is excessively humid, and transpiratory loss is correspondingly reduced; but assimilatory decomposition of water continues, and if this coincides with obstruction to the passage of liquid along the water-vascular system, a certain amount of decrease in turgescence must necessarily ensue. The decrease, however, is inconsiderable, and under normal circumstances, neither alone nor in co-operation with decrease due to coincidently increased transpiratory loss, does it suffice to determine the full assumption of the nocturnal position. It is only under the coincident influences of dry soil, dry air, and insolation that the full nocturnal position is spontaneously attained during the day: in other words, it is only attained under circumstances which imply defective root-supply, gaseous obstruction of the water-vascular system, and excessive transpiratory loss.

The position of the various parts of very young leaves, in which periodic movements have not yet begun to manifest themselves, is as follows —The primary petiole is extremely divergent from the line of the axis, so that, where the latter is vertical it is either slightly ascending, horizontal, or slightly depressed (Plate I, Figs 11, 12, 18 , Plate V, Fig 14) The pinnæ are closely convergent and bent backwards at an acute angle over the upper surface of the primary petiole, the rachises of the basal pair usually having their upper surfaces directed more or less inwards, so that the edges of the closely folded pinnules are directed obliquely outwards and inwards in place of directly upwards and downwards, and the distal pinnæ are overlapped and partially concealed The pinnules, which from the outset are fully expanded, are closely convergent, and have their midribs directed upwards and forwards at an acute angle to the line of the secondary rachises As time goes on, the primary petiole lengthens, but retains its previous position to the axis, and the pinnæ gradually become first erected and then bent backwards, so as to lie in the same plane as the primary petiole or slightly ascending from it, and at the same time become slightly divergent (Plate I, Figs 11, 12, 18) When periodic movements first appear they are for a time confined solely to the primary petiole, which during the day undergoes elevation or convergence towards the axis, and nocturnally returns to its original position of extreme divergence or slight deflection The amount of diurnal displacement is at first very small, but undergoes rapid increase, and with this movements determining diurnal divergence and nocturnal convergence of the pinnæ begin to manifest themselves Finally, movements appear in the pinnules also, leading to steadily increasing diurnal divergence and depression and to a certain amount of rotation downwards of the posterior or outer half of the lamina alternating with nocturnal convergence, elevation, and reverse rotation When movements are at a maximum, the diurnal and nocturnal positions of the various parts of the leaves are normally as follow —Diurnally the primary petiole usually lies at an acute angle to the axis, but the degree of convergence varies greatly in different instances and under differing conditions, owing to the influence of variations in the amount of the leverage exerted by the distal parts of the leaf The pinnæ lie almost in the same plane as the primary petiole or slightly ascending from it and are widely divergent, the divergence of the basal ones being frequently so great as to exceed a right angle, so that they are directed slightly backwards (Plate V, Fig 12) The pinnules lie with their upper surfaces facing directly upwards and their midribs widely divergent (Plate V, Figs 2, 4) The divergence varies in different parts of the pinna the lower pinnules being frequently directed somewhat backwards, the central ones at right angles to the secondary rachis, and the distal ones inclining forwards As the pinnules are set on very closely, the intervals between them falling very considerably short of the breadth of individual laminæ, it is very seldom that the entire surface of any pinnule is entirely exposed, and, as a rule a certain amount of the anterior half of each successive lamina is concealed by the posterior half of the succeeding one (Plate V, Fig 3) In the maximal normal nocturnal position determined solely by absence of photic stimulation, the primary petioles lie nearly at right angles to the axis, that is, in cases where the latter is vertical, some are horizontal, others slightly ascending and still others slightly descending The secondary rachises are closely convergent and slightly elevated, and the lower pair are rotated, so that their upper surfaces are directed more or less inwards The pinnules are closely convergent, so that the two rows are in contact with one another, the upper surfaces of the laminæ facing directly inwards and the lower ones directly outwards (Plate V,

Fig. 1). The midrib is directed upwards and forwards at an acute angle to the line of the secondary rachis, so that the true posterior or outer surface of the keel faces upwards and backwards, and the anterior, or axillary surface, downwards and forwards. The movement accompanying the transition from the diurnal to the nocturnal position is thus evidently not of the simple nature of that in the pinnules of *Pithecolobium*, but one in which convergent elevation is combined with rotation as it is in the pinnæ of *Cassia alata* or the pinnules of *Leucæna glauca*. The ultimate depression of the midrib which is so conspicuous in them is, however, absent, apparently in relation to the absence of such a considerable accumulation of pulvinar parenchyma over the base of the under surface of the outer half of the lamina, and therefore to the upper side of the keel of the midrib in its rotated position, as is present there.

The phenomena of periodic movements in *Mimosa pudica* once more afford a striking example of the fact that the assumption of the diurnal position implies a departure from a previously permanent one, and assumption of the nocturnal one a return to it. This holds good for every part of the leaves, for, although according to ordinarily accepted belief, the normal nocturnal position of the primary petioles is one of deep depression, this is most certainly not the case in healthy plants exposed to natural conditions and which have not been exposed to any disturbance.

Under such circumstances the nocturnal position of the primary petioles is one of pure reversion to the originally permanent one of slight elevation (Plate V, Fig. 14), horizontality, or slight depression; but it differs from it in being a very unstable one which is very readily replaced by one of extreme depression. Very slight mechanical disturbance is enough to secure displacement from it, and it is, therefore, only on still evenings that the leaves retain their normal position as determined solely by absence of solar stimulation. Deep depression of the primary petioles is not a normal nyctitropic phenomenon in healthy plants exposed to natural conditions, and when it is present it is owing to precisely the same causes which give rise to its appearance during the day. The causes act with great readiness because the normal nocturnal position is one of extreme instability, connected with depression of osmotic property in the pulvinar parenchyma which makes for elevation (*vide* Appendix C), but they do not differ in nature from those acting diurnally in any respect. Under these circumstances it is a matter of surprise to find such a skilled observer as Sachs asserting that there is a difference in the condition of the pulvinar tissues according as the position of deep depression is a nocturnal or a diurnal one. According to him diurnal depression following the incidence of mechanical impulses or other so-called stimulant agencies is associated with diminished turgescence of the pulvinar tissues, so that the leaf swings freely in pendulum fashion; whilst in nocturnal depression no such diminution occurs, and the position is a rigid one.* As the position in any case has precisely the same causation, it would be strange indeed were any such difference present, but as a matter of fact it is not. This is only an example of various authoritative statements regarding the phenomena presented by the leaves of *Mimosa pudica*, which are most certainly absolutely incorrect as regards plants grown under normal circumstances (*Vide* Appendix D). The phenomena may present themselves in the case of pot-plants with limited root supply and exposed to the abnormal atmospheric conditions ordinarily present in conservatories, but they certainly are not present under natural conditions, and therefore cannot be regarded as normal to the plant.

* Sachs, Vorlesung, XXXVII, s. 789.

The periodic movements of the leaves of *Mimosa pudica* are not only typically nyctitropic in respect of the nocturnal position being one of reversion to a previously permanent one, but also in respect of the phenomenon of the attainment of the maximal nocturnal position during the first part of the night and gradual departure from it subsequently quite apart from any photic influence The amount of reversion towards the diurnal position exhibited by the pinnæ and pinnules is comparatively slight, but elevation of the primary petiole during the later hours of the night advances so far that in plants exposed to normal conditions the maximal elevation for the twenty four hours is attained immediately before sunrise This at first sight appears to be an anomalous phenomenon, but in reality it may be readily accounted for The maximal elevation which occurs before sunrise is not to be regarded as indicating that the inferior parenchymal tissue of the primary pulvinus then attains it maximal turgescence, and, consequently, its maximal strength It merely indicates the presence of relative maximal strength in relation to distal leverage The inferior mass of pulvinar parenchyma has constantly not merely to contend with the depressant action of the superior one, but also against the leverage of the distal portions of the leaf Both of these are subject to variations, and the action of the leverage is so important as an agent in determining the exact position at any given time that any considerable reduction of distal weight may not merely equilibrate a temporary increase in relative strength of the superior mass of pulvinar parenchyma, but may well go farther and secure that the entire resistance which the inferior mass has to overcome shall actually attain a minimum under the circumstances

The importance of distal leverage as a factor in affecting the position of the primary petiole quite apart from any alterations in the relative strength of the opposing masses of pulvinar parenchyma, is indicated very clearly by the phenomena which follow amputation of the pinnæ of fully expanded leaves (*vide* Appendix A) The first effect of this normally is to give rise to rapid and excessive depression of the petiole, but elevation soon sets in and advances so far that the petiole not merely rapidly regains its original position, but becomes much more elevated or convergent to the line of the axis, than it was whilst the leaf was intact The effects of alterations in distal leverage on the position of the primary petiole are also very conspicuous in cases in which the pinnæ, in place of being removed, are merely exposed to conditions determining considerable diminution in their weight When a plant, the leaves of which are fully expanded, is suddenly transferred to an atmosphere very much drier and considerably warmer than that to which it had previously been exposed, elevation of the pinnules begins almost immediately and advances rapidly until they have completely assumed the nocturnal position This phenomenon is clearly owing to loss in active turgescence connected with sudden and excessive transpiratory loss accompanied by obstructive expansion of the gaseous contents of the water vascular system But the primary petioles show no tendency to assume the position proper to the early part of the night They show no tendency towards depression, but, on the contrary, gradually become very highly elevated It cannot be imagined that this is the result of any increase in the absolute strength of the mass of inferior pulvinar parenchyma which makes for elevation The tissues in the pulvini, whether petiolar or pinnular, must alike be subject to diminution in turgescence and consequent loss of absolute strength under the circumstances to which the plant is exposed, but the loss in strength in those pulvinar tissues in the primary pulvinus which make for elevation is more than counterbalanced by the excessive

transpiratory loss in weight and leverage of the pinnæ, and this is of course equivalent to increased relative strength in the portions of the primary pulvinus which make for elevation.

The excessive elevation of the primary petioles during the later hours of the night is owing to a similar disturbance in the relations existing between pulvinar strength and distal leverage. The diminution in distal leverage in this case is not, however, owing to excessive transpiratory loss in the distal parts of the leaves, but to continued absence of assimilation and coincident continued respiratory loss. The position of the primary petioles at sunset is no doubt partially determined by the fact that the inferior mass of parenchyma contains an excess of tissue liable to rapid filtrative loss of fluid on the cessation of the active assimilatory formation of unstable osmotic products consequent on removal of solar stimulation, whilst transpiratory loss continues to proceed, and a certain amount of departure from the maximal nocturnal position might naturally be expected to occur under the influence of cessation of transpiratory loss and continued root-supply. The departure would not, however, proceed so far as it does and lead to maximal elevation just before sunrise, were it not for the steady decrease in weight of the distal portions of the leaf dependent on continued respiratory loss; for the hours of darkness correspond to a period of fasting during which continuous expenditure takes place without corresponding addition of new materials derived from extraneous sources, and consequently loss in weight must occur. On renewed solar stimulation the pulvinar tissue increases in turgescence and absolute strength, and the inferior mass of parenchyma undergoes relative increase in strength in respect to the superior one, but not in proportion to the increased weight of the distal parts of the leaf which takes place in consequence not merely of their increased turgescence, but to the gradual accumulation of fixed products of assimilation which takes place within them under the influence of sunlight. Maximal elevation can thus no longer be maintained, but progressive descent sets in and attains a maximum when the removal of solar stimulation occasions general loss in turgescence at a period when the accumulation of the fixed products of active assimilation has attained its maximum. The accumulation of assimilatory products in the pulvinar tissues does not render them more powerful to resist leverage save in so far as it affects the osmotic properties of the cell-sap; but the accumulation within the distal parts of the leaf renders them heavier, and therefore more resistant to the elevating action of the inferior mass of pulvinar parenchyma.

No such anomalously excessive departure from the primary nocturnal position occurs in the secondary rachises and pinnules. The reversion towards the nocturnal position exhibited by them during the later parts of the night is limited in extent and is of precisely the same nature and origin as that occurring in nyctitropic structures generally. It is owing simply to the fact that, on the removal of solar stimulation, greater filtrative loss of fluid takes place from those tissues which make for the diurnal position than from their structurally stronger opponents during the period in which active transpiration continues, and that during the succeeding period of continued absence of transpiration and uninterrupted root-supply all the tissues alike have the opportunity of fully satisfying the osmotic capacity which they possess apart from solar stimulation, which implies a certain amount of increase in relative strength in the tissues which make for the diurnal position and which had previously suffered most from filtrative loss. But, in the case of the primary pulvini, this occurs during a period in which the tissue which gains in

relative strength is opposed by progressively diminishing distal leverage which is equivalent to its undergoing progressive and additional increments in relative strength.

The structural features in the motor organs of *Mimosa pudica* which determine the occurrence of the various periodic movements are parallel to those which we have already found to be characteristic of those of other nyctitropic leaves. As in the case of the latter, the opposing masses of pulvinar parenchyma appear at a relatively late period in the development of the leaf and are not developed simultaneously, the development of the masses which make for the diurnal position lagging behind that of their opponents. In the case of the primary pulvinus the antecedent development of the mass of tissue which makes for the nocturnal position is clearly indicated by the fact that, for a considerable time ere periodic movements set in, a process of continuously increasing divergence of the primary petiole from the line of the axis manifests itself, which ultimately leads to its assuming a permanent position corresponding to the primary nocturnal position of a later stage of development. At first sight it might appear as though the permanence of the position were anomalous, and as though movements of nocturnal convergence similar to those occurring in young leaves of *Pithecolobium* ought to attend the nocturnal loss in turgescence of the growing mass of parenchyma overlying the vascular axis of the pulvinus. There is, however, no appreciable evidence of their occurrence, and as a matter of fact there is no reason why they should occur.

The conditions are not parallel in the two cases. In *Pithecolobium saman* the mass of pulvinar tissue which leads to divergence has not only to overcome the resistance of a relatively strong vascular axis, but also that of an antecedently developed mass of pulvinar parenchyma making for elevation, whereas in *Mimosa pudica*, during the period at which progressive divergence of the primary petiole advances continuously, the accumulation of pulvinar tissue making for convergence has not yet begun to make its appearance, and the axial cord of vascular tissue is very weak, and from its flattened form, specially flexible in a vertical direction, so that, so long as it is unaided, it is incapable of producing any appreciable effect in resisting the pressure of the axillary parenchyma aided by the rapidly increasing leverage of the distal portions of the leaf bearing on the continuously elongating petiolar lever.

In the mature primary pulvini the axis consists of a solid cord of soft flexible wood, surrounded by a sheath of bast and containing no medullary tissue. It is compressed vertically, so as to present an oval figure with the long diameter horizontal, and is surrounded by a thick mass of parenchyma (Plate VI, Figs 2, 5b). As the outline of the pulvinus as a whole is more circular, it necessarily follows that the masses of parenchyma lying to either side of the fibro-vascular axis are thinner than those which lie above and below it. The latter, moreover, are not of equal thickness, for the superior one is only slightly thicker than the fibro-vascular bundle, while the inferior one is considerably so (Plate VI, Figs 1, 2, 5b). The vertical measurements of the masses above and below the fibro-vascular bundle of the latter, and of the pulvinus as a whole, in the specimen illustrated in the figure were as follow:—

Vertical thickness of	entire pulvinus	1.74	m.m.
,, ,,	upper parenchyma	0.57	,,
,, ,,	fibro-vascular bundle	0.51	,,
,, ,,	lower parenchyma	0.66	,,

The measurements in a section derived from another pulvinus were the following :—

Vertical diameter of the entire pulvinus	... ...	1·59 m.m.
„ „ „ upper parenchyma	... ...	0·54 „
„ „ „ fibro-vascular axis	... ...	0·45 „
„ „ „ lower parenchyma	... ...	0·60 „
Thickness of cell-walls in superior parenchyma =	...	0·0036 to 0·0054 „
„ „ „ inferior parenchyma =	... ...	0·0018 „
Transverse diameter of the entire pulvinus	... ...	1·77 „
„ „ „ lateral parenchyma	... ...	0·57 „
„ „ „ fibro-vascular axis	... ...	0·63 „
„ „ „ lateral parenchyma	... ...	0·57 „

These figures very clearly show the vertical compression of the pulvinus as a whole, and also the excess in vertical compression of the fibro-vascular bundle, the horizontal diameter exceeding the vertical one by only 10·8 per cent. in the former and by 22·6 per cent. in the latter case.

This, however, is not the only difference between the opposed masses of parenchyma which make respectively for elevation and depression. Both are alike in being composed of two distinct strata of tissue. The outer of these is relatively dense in texture, the individual cells being separated from one another only by minute angular intercellular spaces like those present in the pulvinar parenchyma of *Pithecolobium saman* and *Leucæna glauca*, while the inner one is of very open character, being permeated throughout by a very extensive and highly developed system of huge intercellular spaces (Plate VI, Figs. 3, 4, 12). The characters of the cell-walls also differ in the two strata. In the outer one they are provided with numerous small pits like those in the walls of the pulvinar cells of the other nyctitropic leaves which have been previously described; but in the inner one, in addition to such pits, they are provided with others of a much more elaborate character and of much greater size. The latter pits have a more or less circular or oval outline and a thickened rim, and are closed by a delicate membrane which in its turn shows secondary pits or actual orifices of small size and varied outline (Plate VI, Figs. 3, 4, 12). The majority of these large pits appear to be situated so as to abut on portions of neighbouring cells, but some of them appear to be in direct relation to the great intercellular spaces of the tissue. The walls of the cells entering into the constitution of the outer stratum of tissue of the parenchyma lying above the fibro-vascular bundle are about twice as thick as those of the corresponding stratum lying beneath it. The walls of the cells in the deeper strata both above and below the fibro-vascular axis do not differ from one another to any appreciable extent, and are alike of very considerable thickness save within the areas of the pits. The cells throughout the entire thickness of the parenchyma both above and below the bundle contain chlorophyll, but the numbers of chromatophores in the cells of the deeper stratum of tissue are much greater than those in the superficial one, and this implies a corresponding excess of chlorophyll in the inferior as compared with the superior mass, seeing that the excess in thickness which the former presents is entirely owing to an excess in the thickness in the deeper stratum of its tissue, the thickness of the superficial stratum being alike both above and below the fibro-vascular axis. The line of demarcation between the two strata of tissue is rendered very conspicuous, even under very low magnifying powers, in sections which have been momentarily immersed in a 2 per cent.

aqueous solution of osmic acid and mounted in saturated solution of acetate of potash The superficial stratum then acquires a strong brown madder tint, whilst the deeper one remains almost unaltered in colour, and sections which have been treated in this fashion consequently afford a very clear demonstration of the distribution of the two strata throughout the pulvinus, and of the fact that the excess in thickness of the inferior mass of parenchyma is owing to the deeper stratum of tissue on its attaining a greater thickness than it does in the superior one (Plate VI, Figs 1, 2) The distinction between the two strata of the parenchyma comes out less clearly, but is still quite recognisable, in preparations which have been subsequently stained with picrocarmine (Plate VI, Fig 6)

The structural features presented by the primary pulvinus of *Mimosa pudica* are thus of a nature readily to account for the occurrence of periodic movements in the primary petiole The persistently soft, flexible consistence of the fibro vascular bundle, its vertical compression, and its relatively small bulk in relation to the masses of pulvinar parenchyma, unite to render it peculiarly liable to vertical flexion in connection with alterations in the relative strength of the over and under lying masses of tissue, and the structural peculiarities which the latter present secure that such fluctuations shall occur The characters of the cell walls in the superficial strata in the superior and inferior parenchyma imply an excess of structural strength in the former, and the greater thickness of the deeper stratum in the inferior parenchyma secures an excess of functional strength and additional structural weakness in it Owing to its textural peculiarities, the inferior mass of parenchyma must necessarily be liable not only to much greater but to much more rapid fluctuations in turgescence than the superior one, the greater mass of tissue rich in chlorophyll accounting for its liability to excess in fluctuations of turgescence, and the excess of tissue providing *special facilities for filtration allowing for such fluctuations taking* place in large amount with great rapidity The greater thickness in the cell walls of the outer stratum of the parenchyma lying above the fibro vascular axis confers greater structural strength on it than that which is provided by the textural features of the corresponding stratum on the underside of the pulvinus, and the excess in thickness of the deeper stratum in the mass lying beneath the axis secures greater functional strength and also greater facilities for rapid filtrative loss of turgescence there, owing to the excess which it implies of open and elaborately pitted tissue abundantly provided with chlorophyll There is nothing to lead to the belief that the individual elements in the deeper stratum of parenchyma are likely to undergo greater turgescence under solar stimulation in that portion of it underlying the fibro vascular axis than in that which lies above the latter, but the number of elements present in the former site considerably exceeds that in the latter, so that under solar stimulation a greater general rise in turgescence must occur in the inferior than in the superior parenchyma as a whole Conversely the loss in turgescence attending removal of solar stimulation must give rise to greater total loss of turgescence in the lower than in the upper or axillary mass of parenchyma, and therefore, apart from any interfering factors, solar stimulation would necessarily give rise to convergence or elevation of the petiole, and absence of such stimulation to divergence or depression But, as has been already pointed out, a very powerful interfering factor is provided by the variations in weight of the distal parts of the leaf The leverage exerted by the distal parts of the leaf co operates constantly with the axillary mass of parenchyma in making for depression, it is not, however, a constant quantity, but one which is subject to undergo very considerable variations It is a factor the power of which normally rises

under the same circumstances as the strength of the mass of pulvinar parenchyma making for elevation increases, and hence, under normal circumstances, maximal elevation of the primary petiole does not coincide with maximal strength of the parenchyma making for elevation. The strength of the latter, in so far as it has to contend with the opposing mass of pulvinar parenchyma, rises under the influence of solar stimulation; but this increase is apparently more than discounted by the coincident rise in distal leverage, so that, although its strength attains an absolute maximum under such circumstances, the tissue is relatively weaker in respect to the total resistance which it has to overcome than it is under the influence of continued absence of photic stimulation.

The structural peculiarities of the leaves of *Mimosa pudica* do not, however, merely provide facilities for the occurrence of extensive movements of the primary petiole in connection with variations in the degree of solar stimulation of assimilatory function in the tissues, but also for the ready occurrence of such movements under the influence of various other conditions. The primary petiole is constantly in a position of extremely unstable equilibrium which is determined by the action of the superior pulvinar parenchyma and the leverage of the distal parts of the leaf on one hand, and of that of the inferior pulvinar parenchyma on the other. Any alterations in distal leverage or in the relative strengths of the opposing masses of parenchyma must inevitably lead to movements of the petiole in one direction or another. Any increase in distal leverage must tend to induce depression or divergence of the petiole, not merely in connection with coincident compression of the tissue of the inferior pulvinar parenchyma, but because of the increased filtrative loss of turgescence which this implies; and any decreased leverage to corresponding elevation up to the point at which the cells of the inferior parenchyma have attained the greatest degree of turgescent increase in capacity of which they are capable. But variations in distal leverage do not take place solely in connection with variations in the conditions of assimilatory activity of the tissues. Any addition of weight to the distal portions of the leaf whether of intrinsic or extrinsic origin, or any additional pressure on the upper surface of the petiole, imply corresponding increments of leverage, and hence we find that, especially when these are developed suddenly, they are liable to be followed by depression of the leaf. On the other hand, we have already seen how rapid loss of weight in the distal parts of the leaves, as the result of excessive evaporation there, may lead to extensive movements of elevation.

The tissues of the primary pulvinus not only provide facilities for the occurrence of extensive movements in the primary petioles, but they are further especially adapted to permit of these movements being executed with great rapidity under certain circumstances. The fibro-vascular bundle is permanently weak, soft and flexible, and the mass of pulvinar parenchyma which underlies it presents excessive structural facilities for rapid filtrative redistribution of large masses of fluid within its deeper stratum, with its thick-walled and elaborately pitted cells and great system of intercellular spaces. We have already seen that rate of movement is directly related to the degree in which the pulvinar tissues present structural peculiarities favouring rapid alterations in turgescence, and that the tissues in the primary pulvini (and specially in those portions of parenchyma underlying the fibro-vascular axis of the primary pulvini of *Mimosa pudica*) are endowed with such peculiarities in exceptionally high degree. The superior mass of pulvinar parenchyma, aided by the leverage of the distal parts of the leaf, is constantly making strongly for depression of the primary petiole. Elevation is only maintained by means of active

turgescence of the inferior parenchyma sustained in spite of excessive local facilities for rapid filtrative escape of fluid and the combined compressant action of the superior parenchyma and distal leverage, so that anything giving rise to sudden loss of osmotic property in the cell sap, to sudden diminution in the supply of fluid to satisfy the osmotic capacity of the latter, or to sudden increase in the conditions of local pressure affecting filtration must inevitably lead to sudden movements Active turgescence of the excessively porous tissue of the deeper stratum of pulvinar parenchyma can only be maintained as the result of the continuous addition of highly osmotic and unstable assimilatory products to the cell sap with coincident abundant supply of fluid to make good the constant filtrative loss which is going on in the tissue, and it is only under conditions of high turgescence that the inferior mass of pulvinar parenchyma is able to overcome the conjoint action of the superior mass and of distal leverage so long as the latter is maintained at a high level The superior mass of parenchyma is not devoid of tissue presenting special facilities for rapid redistribution of fluid, but it contains much less of such tissue than the superior one does, and hence any conditions determining general loss in turgescence must produce greater and more rapid weakening of the inferior than of the superior mass Under ordinary circumstances the loss of strength in the superior mass is thus concealed by the greater loss taking place in the inferior one, and it is only where the action of any agent inducing a fall in turgescence is carefully limited to the superior mass that we have any indices to its action upon it (*vide* Appendix B)

The structural peculiarities permitting of the occurrence of rapid loss in turgescence in the inferior mass of pulvinar tissue also permit of rapid gain, processes of rapid endosmose being provided for by the excessively porous character of the cell walls and the abundant chlorophyll contents of the deeper stratum of tissue The process of elevation is of course, never so rapid as that of depression, because it is resisted by distal leverage and is mainly carried out by osmosis in place of filtration, but in spite of this it is very much more rapidly conducted than it is in cases where the pulvinar tissues do not provide the same facilities for rapid absorption of fluid, and under favourable circumstances of illumination and water supply, its progress is readily visible to the unaided eye (*vide* Appendix B)

The structural peculiarities of the inferior masses of pulvinar parenchyma in the primary pulvini of *Mimosa pudica* unequivocally provide facilities for the occurrence of sudden loss of turgescence in the tissue, but the movements in the primary petioles are not invariably suddenly executed The capacity for the occurrence of sudden movements is dependent on the presence of certain structural peculiarities facilitating rapid movements of fluid in the tissues, but the actual occurrence of sudden movements even in cases where such peculiarities are present in very high degree, depends on the sudden incidence of conditions making for the redistribution of fluid Hence in *Mimosa pudica* any gradual diminution in water supply only causes gradual movements in the primary petiole in spite of the excessive textural facilities for escape of fluid from the tissues of their motor organs, and, further than this the effects of gradual local alterations in turgescence in the latter may be more than discounted by coincident alterations in distal leverage, so that elevation in place of depression may occur It is only under such circumstances, however, that movements of this reversed character are present in connection with loss of strength in the inferior as compared with the superior pulvinar parenchyma They never occur in connection with conditions implying local increase in

filtrative escape of fluid from the inferior pulvinar tissues dependent on local increments of external pressure there. Such increments do not, of course, affect the leverage of the distal portions of the leaf, but merely give rise to modifications in the relative strengths of the opposed masses of pulvinar parenchyma of such a nature as to confer increased relative strength upon the superior one; and hence the movement of the petiole follows a normal course and depression results.

The secondary pulvini differ structurally in many respects from the primary ones, and much more closely resemble the pulvini of common nyctitropic leaves than the latter do. The fibro-vascular axis, like that of the primary pulvinus, has the form of a solid cord devoid of any medullary content, but it is only slightly flattened vertically, and therefore presents no special facilities for flexion in one direction rather than another (Plate VI, Fig. 5*a*). The following figures show the measurements of the various portions of two sections derived from distinct pulvini; the line of section in the first case having fallen parallel with the length of the fibro-vascular bundle (Plate VI, Figs. 7, 8), and in the second at right angles to it (Plate VI, Fig. 5*a*)—

Section 1.—Total breadth of pulvinus	1·005	m.m.
Breadth of external mass of parenchyma	0·33	„
„ fibro-vascular bundle	0·33	„
„ axillary mass of parenchyma	0·345	„
Section 2.—Transverse diameter of entire pulvinus	1·08	„
„ „ of outer parenchyma ...	0·33	„
„ „ of fibro-vascular bundle. ...	0·39	„
„ „ of axillary parenchyma ...	0·36	„
Thickness of cell-walls on the outer mass of parenchyma	0·0018 to 0·0036	„
„ of cell-walls in axillary mass of parenchyma	0·0018 to 0·0027	„
Vertical diameter of entire pulvinus	1·11	„
„ „ superior parenchyma	0 39	„
„ „ fibro-vascular bundle	0·33	„
„ „ inferior parenchyma	0·39	„

These figures show that the fibro-vascular bundle is much more rounded than in the primary pulvinus, and relatively strong in relation to the surrounding parenchyma in every direction; and also that the pulvinus as a whole, in place of being flattened vertically, is somewhat compressed laterally. The horizontal diameter of the fibro-vascular bundle sometimes, as in the second section, slightly exceeds that of either of the lateral masses of parenchyma and, in other cases, falls slightly short of that of the inner one, as in the first section. The walls of the cells in the outer mass of parenchyma are somewhat thicker than they are in the axillary one, but no such conspicuous difference in this respect is present here as in the case of the cell-walls in the superior and inferior parenchyma of the primary pulvinus. The tissue of the internal or axillary mass is slightly richer in chlorophyll than that of the outer one. There is no evidence of the presence of two structurally distinct layers in the thickness of the parenchyma. It darkens uniformly down to the bundle-sheath under treatment with some acid, and there is an entire absence of any great system of intercellular spaces like that in the deeper stratum in the parenchyma of the primary pulvinus. A certain number of cells provided with large and elaborate pits is, however, present in the immediate neighbourhood of the bundle-sheath; but these cells do not form a continuous layer, and they are irregularly distributed. The only features, then, which distinguish the axillary from the outer mass of

parenchyma, are slight excess in bulk (Plate VI, Fig 7) slight excess in the thickness of the walls of the constituent cells, and slight excess in chlorophyll content There are no intrinsic structural features in the secondary pulvini implying such instability in equilibrium of position as there are in the primary ones, and, in addition, so long as the primary petiole is not deeply depressed, distal leverage does not come into play as an extrinsic factor of disturbance and with this we find much less liability to the occurrence of extensive and especially of rapid extensive movements in the secondary rachises than in the primary petiole Very considerable periodic movements of divergence and convergence are regularly carried out as in other nyctitropic leaves in connection with the incidence or removal of solar stimulation, but there is very much less tendency to the occurrence of extensive and rapid movements under the influence of other factors than there is in the case of the primary petioles and pinnules—conditions which determine the fullest depression of the primary petioles and maximal movements of the pinnules often leaving the secondary rachises almost entirely unaffected (Plate V, Figs 12, 13), and, if the intrinsic structural peculiarities of the tissues of the secondary pulvini alone be taken into account this is not so much a matter for surprise as that extensive movements should occur at all The opposing masses of pulvinar parenchyma acting on the relatively strong fibro vascular cord differ so slightly in character from one another that, if attention be limited to them it would be hard to explain the occurrence even of regular nyctitropic movements of an extensive character There are no intrinsic structural peculiarities present in the pulvini to justify us in supposing that any very considerable fluctuations in the relative strengths of the axillary and external masses of pulvinar parenchyma take place, and in spite of this, very extensive movements of convergence and divergence regularly succeed one another every evening and morning When, however, the relations of the opposing masses of parenchyma to neighbouring parts are taken into account, this apparent anomaly disappears (Plate VI, Figs 9, 10, 11) The base of the outer mass of parenchyma is in immediate contact with a mass of tissue projecting in bracket fashion from the axis, and composed of very delicate cells poor in protoplasm and specially poor in chromatophores The lower portions of the axillary masses, on the other hand, are either in close contact with the side of the rachis, which presents little compressable tissue, or in the case of terminal pulvini, with the corresponding mass of the neighbouring pulvinus The bracket or cushion on which the base of the outer mass rests is composed of tissue which is weak alike structurally and functionally, and consequently presents little resistance to compression, so that, when turgescence rises in the axillary parenchyma displacement is effected not so much by compression of the tissue of the outer parenchyma as by compression of the bracket upon which it rests There is probably only an inconsiderable excess in rise in turgescence in the axillary mass as compared with the outer one under the influence of solar stimulation, but the rise that does occur acts at an advantage in effecting displacement because it has a resistent basis to work upon The turgescent tissue of the axillary parenchyma is supported by the resistance of the lateral surface of the rachis or by the equally turgescent tissue of the neighbouring pulvinus, whereas the external parenchyma rests on an insecure foundation, and readily sustains displacement From its relations to neighbouring parts the axillary tissue, when its turgescence rises under solar stimulation, is able to overcome the resistance of the relatively strong, passively convergent fibro vascular bundle, which receives little support from the external parenchyma owing to the insecure foundation on which the latter rests The struggle

in this case also is one which is principally maintained between the fibro-vascular tissue and the axillary parenchyma, the external parenchyma from its unstable foundation being incapable of making actively for convergence to any considerable extent. There is therefore no difficulty in seeing why rise in turgescence in the pulvinar parenchyma, although it be fairly uniformly distributed, should be followed by movements of divergence of very considerable magnitude; and there are structural reasons to account for the fact that, as a rule, movements of any kind should be conducted only gradually. Both in their structural features, and in the characters of the movements which they give rise to, the secondary pulvini of *Mimosa pudica* much more closely resemble the pulvini of common nyctitropic leaves than either the primary or tertiary pulvini do. The amount of tissue favouring exceptionally rapid redistribution of fluid which they contain is trifling in comparison to that present in the primary pulvini, and it is not normally exposed to nearly so much resistance as it is in these. In the primary pulvini there is an abundance of tissue liable to exceptionally rapid filtrative loss in turgescence, and struggling with excessive resistance dependent on intrinsic pulvinar conditions and distal leverage. In the secondary pulvini both the amount of such tissue and the resistance to which it is exposed are very much less, so that it would be strange indeed were the capacity for rapid movement alike in the two cases. So long as the primary petiole is not deeply depressed, leverage does not come into play in making for convergence of the secondary rachises, and with this we frequently find sudden movements of them almost entirely absent, and, as a rule, at the utmost very limited; but when deep depression of the primary petiole does occur, distal leverage begins to act, and a correspondingly increased tendency to the occurrence of rapid and considerable convergence of the secondary rachises manifests itself under circumstances leading to decreased turgescence in the secondary pulvini.

The tertiary pulvinus differs as strikingly in structural features from the secondary one as the latter do from the primary. The entire organ is greatly compressed vertically so as to present an elongated elliptical figure, and its fibro-vascular bundle has the form of a broad flattened strip traversing the centre of the parenchyma (Plate VI, Fig. 13). The following are the measurements of the various parts of the section from which the figure was obtained:—

Transverse diameter of entire pulvinus	0·735	m.m.
Thickness of parenchyma to the left of the fibro-vascular bundle ...	0·12	,,
Breadth of fibro-vascular bundle	0·48	,,
Thickness of parenchyma to the right of the fibro-vascular bundle...	0·135	,,
Vertical diameter of entire pulvinus	0·39	,,
,, ,, of superior parenchyma	0·18	,,
,, ,, of fibro-vascular bundle	0·06	,,
,, ,, of inferior parenchyma	0·15	,,
Thickness of cell-walls of inferior parenchyma	0·0054	,,
,, ,, ,, of superior ,, ...	0·0009	,,

It is evident that the extreme vertical compression of both the entire pulvinus and of the fibro-vascular bundle provide even greater facilities for vertical flexion than are present in the primary pulvinus. The organ has not, however, to struggle with any excessive distal leverage as the primary pulvinus has, and practically we may regard its position as determined simply by the conflicting forces of the inferior

and superior masses of parenchyma and the normal passive direction of the fibro vascular bundle to the fibro vascular tissue of the secondary rachis

The fibro vascular bundles issue obliquely from the bevelled surfaces on either side of the upper half of the secondary rachis, and are originally directed forwards and slightly upwards from their sites of origin, and horizontally parallel to the line of the rachis (Plate V, Fig 5) Owing to the obliquity of origin of each bundle its upper surface looks upwards and forwards, and its lower one downwards and backwards so long as the original position is maintained or resumed The masses of parenchyma lying above and below the fibro vascular band differ strikingly from one another in structure, and are sharply defined from one another even where they are not separated by the bundle (Plate VI, Fig 13) The superior mass is slightly thicker than its opponent Its component cells have very thin walls and relatively abundant protoplasmic contents, and the tissue is comparatively an open one containing numerous, large, intercellular spaces in addition to minute angular ones The cells of the inferior parenchyma have walls five or six times as thick as those of the superior one (Plate VI, Figs 14—17), the tissue which they compose is a very dense one, and the amount of protoplasm which they contain is relatively trifling in amount The thickness of the cell walls in the superior parenchyma is aobut 0009 m m, that of the inferior one about 0054 m m There is not any considerable difference in the amount of chlorophyll content of the two masses, but the upper one when in a condition of compression, as it ordinarily is in the case of detached pulvini, appears greener than its opponent

The appearances described above can be clearly made out in fresh sections in water or acetate of potash, but are much less distinct in permanently mounted sections unless these have been fixed by treatment with osmic acid ere exposing them to the action of other reagents In order to obtain permanent preparations representing the tissue as far as possible in a natural condition of full turgidity, the freshly cut sections ought to be allowed to be in water exposed to light for some time, so as to allow conditions of turgidity under solar stimulation to be re established, and then immersed for a few seconds in a 2 per cent solution of osmic acid This treatment secures two things—*first*, fixation of the cell walls to some extent, and *second* fixation of the protoplasmic contents of the cell cavities Unless it be adopted the tissue of the superior pad will certainly be more or less shrivelled and collapsed and the cell walls of the inferior one will lose the greater part of their thickness The most satisfactory permanent preparations are those which, after being stained with picrocarmine are mounted in Farrant's solution, but even those mounted in balsam are much more representative of the natural condition of the tissues than any mounted without fixing The greater part of the thickness of the cell walls in the inferior parenchyma is manifestly composed of materials resembling those in the thickened areas in the walls of common collenchymatous tissues, and therefore normally subject to great reduction in bulk on exposure to conditions leading to extraction of water In unfixed sections which are subsequently exposed to immersion in absolute alcohol, &c, prior to mounting in balsam, a complete extraction of water of course, occurs, and with this an excessive reduction in the thickness of the cell walls, and the same effect in somewhat minor degree occurs in unfixed sections mounted in Farrant's solution, but treatment with osmic acid allows of extraction of water without diminution in volume If unfixed

preparations alone are studied, there would appear to be little structural ground for unstability of position in the tertiary pulvini: in fixed ones the structural differences between the opposing masses of tissue are strikingly conspicuous.

The structural peculiarities of the tertiary pulvini thus present maximal facilities for the occurrence of vertical displacement. There is an extremely flattened fibro-vascular bundle, and it is related above and below to large masses of tissue differing from one another in the highest degree in regard to their functional and structural strength. The tissue of the inferior parenchyma presents characters which imply the presence of very considerable and continuous structural strength and of relatively little liability to functional alterations in turgidity. So long as water is supplied to it, the collenchymatous materials in the cell-walls will secure absorption, and consequent maintenance of continuous structural resistance in high degree, whilst the scanty protoplasmic content of the cell-cavities is little calculated to give rise to extensive fluctuations in active functional turgescence. On the occurrence of any sudden diminution or interruption of water-supply, no sudden diminution in the strength of the tissue is likely to occur, because the fluid which is stored up within the substance of the collenchymatous cell-walls cannot be rapidly removed, and, so long as it is present, it opposes an obstruction to the filtrative escape of any fluid from the interior of the cell-cavities, both as the result of the great thickness which it confers upon the cell-walls and the rigidity of texture which its presence implies. In the inferior parenchyma of the tertiary pulvini, we have to deal with a tissue providing not merely for active turgescence of the protoplasts of the cell-cavities, but for very considerable turgescence of the cell-walls. The former is a condition which is at once liable to be affected by fluctuations in assimilatory activity; but the latter bears no direct relation to it, and will remain unaltered so long as sufficient water-supply is present. It is not, therefore, affected by the absence or presence of assimilatory activity, and remains as a constant feature of structural strength both diurnally and nocturnally. On the other hand, the tissue of the superior parenchyma, with its relatively open texture, its very delicate cell-walls, and its abundant protoplasm, provides the conditions for great fluctuations in assimilatory turgescence, and also for the occurrence of processes of rapid filtrative loss. It is constantly opposed by a mass of parenchyma of very much greater structural strength, and by the inherent tendency of the fibro-vascular bundle to resume its original position in relation to the rachis, and it is only under circumstances which call its excess in functional strength into play and provide the requisite supply of fluid to satisfy the osmotic capacities which are developed in the cell-sap as the result of assimilatory activity, that it is capable of overcoming the resistance to which it is exposed. Any depression in general assimilatory activity must weaken it in the struggle which it has to maintain, because its strength is mainly dependent on active protoplasmic turgescence, whereas that of its opponent is predominantly owing to mere physical properties of the cell-walls. But it must also necessarily be weakened under the incidence of any influences giving rise to decrease in the general supply of liquid or favouring filtrative loss because of the structural facilities which it provides for redistribution of liquid in its relatively open texture and the delicacy of the walls of its component cells. The structural peculiarities of the tertiary pulvini as motor apparatus are thus such as to secure the occurrence of regular periodic movements of a strictly nyctitropic character, and also to provide for

the occurrence of both gradual and rapid movements under the influence of any factors affecting supply and loss of water generally, or calculated to give rise to alterations in local filtrative processes

There can be no question that the motor organs of *Mimosa pudica* present structural peculiarities which are of a nature specially to favour the occurrence of movements under the influence of conditions of alterations in turgescence, whether dependent on fluctuations in assimilatory activity, or on variations in conditions affecting general or local supply and loss of fluid, and that the capacity for rapid movement which they severally exhibit bears a direct relation to the textural facilities which they individually offer for rapid filtrative redistribution In the case of the primary pulvinus, very exceptional provision for the occurrence of rapid redistribution of fluid is presented by the deeper stratum of parenchyma, composed as it is of extremely open tissue, built up of elaborately and extensively pitted cells, and in greater part struggling against great resistance, both local and connected with distal leverage In the tertiary pulvini, too, similar facilities are present owing to the excessive delicacy and loose texture of the superior parenchyma which has to contend with the overpowering structural strength of the inferior one and the passive direction of the fibro vascular bundle, and in both primary and tertiary pulvini the capacity for rapid movement reaches a maximal development. In the secondary pulvini, on the other hand, the nature and relatively uniform character of the tissue implies an absence of any structural peculiarities favouring rapid redistribution of liquid in such excessively high degree, and with this we find capacity for rapid movements very much less pronounced A study of the motor organs in *Mimosa pudica* alone thus leads to the same conclusion as that arrived at from the comparative study of the motor organs of nyctitropic leaves generally, that rate of movement is entirely regulated by structural facilities affecting filtrative escape from the interior of the cell cavities of the tissues, whilst amount of movement is dependent on the extent of possible fluctuations in turgescence in opposing masses of tissue It alone is enough to show how erroneous the idea is that, in the opposing masses of tissue in pulvini, we have to deal with differences depending solely on invisible molecular structure, and not on the presence of any visible differences in organisation *

CHAPTER XI.

Theories regarding the movements of the leaves of Mimosa pudica.

In the preceding chapter an attempt has been made to demonstrate that the movements which are conducted by the leaves of *Mimosa pudica* are essentially the same in nature and origin as those which are conducted by nyctitropic leaves generally, and that any peculiarities which they present are to be ascribed to structural features in the motor organs permitting of exceptionally rapid redistributions of fluid throughout the tissues This view is, however, entirely opposed to ordinarily accepted belief, for, although the regular periodic movements are commonly allowed to owe their origin to the same causes as those which determine the occurrence of similar movements in other nyctitropic leaves, the sudden movements arising under other circumstances than those

* Es handelt sich also auch hier wieder nicht um sichtbare Organisationsverhältnisse aus denen sich die Reizbarkeit erklärt sondern um die unsichtbare Molekulstruktur Sachs Vorlesung XXXVI s 770

affecting the presence or absence of solar stimulation have constantly been regarded as of an entirely peculiar and specific nature. The ordinary periodic movements are recognised as being connected with alterations in turgescence dependent on the presence or absence of solar stimulation; but it has apparently never been questioned that the other class of movements are owing to a certain inherent and peculiar irritability and contractility in the protoplasts of certain areas in the motor organs, which enable them to effect alterations in turgescence, when they are called into activity by various stimulant agencies which are quite incapable of producing any similar effect on the protoplasts of the motor organs of common nyctitropic leaves.

The motor organs of *Mimosa pudica* are, in fact, commonly regarded as being provided with a sort of undifferentiated muscular apparatus, and the faith in the existence of this has been so implicit that within recent years an attempt was even made to ascribe the phenomenon of propagation of movement from one part of the plant to another, to the presence of an undifferentiated nervous system provided by the continuity of the protoplasts of the various tissue-elements.* This latter theory hardly merits discussion, as it was very soon demonstrated that protoplasmic continuity is a phenomenon of almost universal occurrence in vegetable tissues, and that the phenomena of propagation of movement in *Mimosa pudica* are in many instances quite inexplicable as the result of any changes occurring along the course of any continuous tracts of living protoplasm. The theory affords, however, an evidence of the fixed belief in the presence of certain specific functional peculiarities in the motor organs of the plant, and its abandonment only led to a renewed search for other possible agencies which might be regarded as capable of calling these into play.†

The belief in the presence of certain specific irritable and contractile apparatus within the motor organs of *Mimosa pudica* appears to have arisen mainly in consequence of the exceptional ease with which movements may, under certain circumstances, be induced, the exceptional rapidity with which they may be carried out, and the extent to which they may be propagated from one part of the plant to another; for, as has already been pointed out, their mere magnitude is by no means exceptional, and they agree with those which are conducted by ordinary nyctitropic leaves in leading, as a rule, to the resumption of a position which, at an earlier period in the history of the leaves, was the permanent one. In addition to this, it has to be borne in mind that the investigations in regard to the nature and origin of the movements have in greater part been carried out in plants exposed to unnatural conditions, and consequently liable to exhibit phenomena of more or less abnormal character and limitation, and that they are consequently very imperfectly representative of those proper to the plant when exposed to its normal environment. The phenomena which are ordinarily described as characterising plants cultivated in pots in European conservatories and laboratories, as has been already pointed out in connection with the question of the initial nocturnal position of the primary petioles, certainly do not correspond in detail to those occurring in plants grown under natural conditions. The artificially-grown plants are subject to the influence of limited root-supply and to abnormal conditions of atmosphere, and it is, therefore, no wonder that the phenomena which they exhibit fail to afford an exact index to those

* Lectures on the Physiology of Plants. By Sydney Howard Vines, M.A., D.Sc., F.R.S. Cambridge, at the University Press, 1886.

† Das Reizleitende Gewebesystem der Sinnpflanze. Von Dr. G. Haberlandt. Leipzig, 1890.

occurring in plants growing under circumstances permitting of indefinite root extension and implying exposure to all possible variations in degree of atmospheric humidity Moreover, it is as a rule only in the tropics that phenomena of foliar movement occur with sufficient frequency, and on a sufficiently large scale, to afford satisfactory opportunities for the comparative study of the peculiarities of movement in many different species, and it is only by means of such comparison that it is possible to determine how far any phenomena occurring in individual cases are really of peculiar and specific nature

The movements which are executed by the leaves of *Mimosa pudica* are exceptional and peculiar as compared with any occurring among nyctitropic leaves in temperate regions, but in any region in which *Neptunia oleracea* occurs, or in which nyctitropic leaves generally abound, it very soon becomes evident that the peculiarity is one of degree and not of kind The movements under certain circumstances are performed with exceptional rapidity, and in connection with the incidence of many slight disturbing influences, but in the leaves of *Neptunia* they may also occur with considerable readiness and rapidity, and in many other common nyctitropic leaves we find examples of movements arising under circumstances similar to those under which the movements of *Mimosa* and *Neptunia* manifest themselves The movements certainly are neither so readily evoked nor so rapidly executed as those of *Mimosa* and *Neptunia*, but the differences in this respect which are present among individual species of common nyctitropic leaves are almost as great as those existing between the movements of certain of them and those of *Neptunia*, and certainly quite as great as those existing between the movements of *Neptunia* and those of *Mimosa* Under favourable circumstances, a single light concussion of a distal pinna may be sufficient to induce complete and very rapid action in a leaf of *Mimosa pudica*, under similar circumstances, slow and limited action of a certain number of pinnules, and possibly a certain amount of convergent movement in the pinna subject to concussion, may occur in the leaves of *Neptunia oleracea* in *Pithecolobium saman* a single concussion fails to produce any appreciable effect but movements arise under the influence of a certain number of repeated concussions, the pinnules gradually rise, the secondary rachises gradually converge and become depressed, and the primary petiole converges where the primary pulvinus retains its activity, finally, in *Cassia alata* very repeated agitation is necessary in order to secure the occurrence of any appreciable movement *in the pinnæ*

Phenomena demonstrating that particular agencies which induce movements in the leaves of *Mimosa pudica* produce a like effect at a different rate in the leaves of other nyctitropic leaves are constantly occurring Separation from the axis under certain circumstances induces rapid and maximal movement in the leaves of *Mimosa pudica* and slow and gradual movements in the case of other nyctitropic leaves, the displacement, whether rapid or retarded, tending invariably to the establishment of the nocturnal position The impact of a single heavy drop of rain is in many cases sufficient to induce maximal movements in the leaves of *Mimosa pudica*, a brief exposure to a heavy shower sends the leaves of *Pithecolobium saman* into the nocturnal position, and prolonged exposure to violent rainfall causes appreciable movements in the pinnæ of *Cassia alata* A single light breath of air may be sufficient to cause maximal movement in *Mimosa pudica*, repeated agitation by a breeze causes the leaves of *Pithecolobium saman* to move towards the nocturnal position, and strong wind produces a like effect in the leaves of *Cassia alata* Under exposure to

the influence of hot dry air and a dry soil, the leaves of *Mimosa pudica*, *Pithecolobium saman* and *Cassia alata* alike assume the nocturnal position, and free supply of water causes them alike to revert towards the diurnal one. All the leaves which have been specially considered in the preceding chapters alike exhibit movements under the influence of certain common conditions, such as exposure to or deprivation of light, excessive transpiration, defective root-supply of water, and mechanical agitation; but they differ greatly from one another in regard to the rate at which they indicate the effect which these conditions produce. But mere differences in onset and rate of movements arising under the influence of like common conditions cannot be taken as any satisfactory evidence that they are owing to different causes, or that the functional properties of the tissues of the motor organs differ from one another in kind. The phenomena afford no sufficient proof of the existence of any essential difference in the functional properties of the tissues, and the structural features of the motor organs are such as satisfactorily to account for the differences which are present in different instances. There is, therefore, every ground for regarding the cause of movement as alike in all cases, and the differences as resulting merely from the rate at which it is possible for it to produce an appreciable effect. Water will escape more rapidly from a vessel with a large orifice than from one with a small one, but this does not show that the cause of escape is different in the two cases.

The structural features of the motor organs of the leaves of *Mimosa pudica* afford no satisfactory grounds for supposing that they are endowed with any peculiar functional properties, and are such as to explain why redistributions of fluid may occur with exceptional rapidity within them; so that there is no reason for the conclusion that the movements which they conduct differ in their nature and origin from those which are conducted by the motor organs of other nyctitropic leaves. They certainly give no sufficient grounds for assuming that the movements are in them, any more than in other nyctitropic leaves, determined by alterations in turgescence depending on active contraction of the protoplasts of the tissues, in place of alterations in the osmotic properties of the cell-sap, alterations in the relations existing between general supply and loss of water, or alterations in conditions affecting local filtration; but they do afford a satisfactory explanation of the fact that the movements should be more rapidly conducted than they are in ordinary nyctitropic leaves. As, however, the belief in the essential dependence of the movements on the exercise of active contraction by certain of the protoplasts in the motor organs is so firmly and widely established, it is desirable that an attempt should be made to determine how far the phenomena of movement themselves really afford any support to it, and how far they are in any way inexplicable as the result of action of the factors which serve to determine the occurrence of movements in other leaves.

In approaching this question it must in the first place be borne in mind that, under normal circumstances, the tissues of *Mimosa pudica* contain an exceptionally large bulk of liquid under very high tension, and that this tension is maintained in spite of exceptional facilities for general transpiratory loss and for local redistributions of masses of water within certain particular areas. It is evident, thus, that all the conditions of unstable equilibrium are present in very high degree, and that the general liquid tension must be liable to undergo constant fluctuations in degree corresponding to any fluctuations in the relations existing between root-supply and transpiratory loss of water. Haberlandt affirms that the liquid, which under most circumstances escapes in such large bulk from the

tissues on section, is entirely derived from the system of seive tubes which he regards as constituting a specific, mechanical nervous system for the propagation of stimulant impulses inducing active contraction of the protoplasts of the motor organs, but, even if it be so, this does not affect the question of the instability of equilibrium between general supply and loss of water. The maintenance of high liquid tension within the seive tubes demands a constant supply of water to satisfy the excessive osmotic capacities of the cell sap which they contain. Their excessive turgescence only implies an additional drain upon the general stock of water which is also subject to excessive transpiratory loss. The presence of any extensive system of tissue elements of exceptionally high osmotic capacities, such as the seive tubes in the bast of *Mimosa pudica*, or the laticiferous tubes of *Euphorbia antiquorum* (Plate VII, Fig. 9), can only serve to render harder the struggle which other less highly endowed elements have to maintain with transpiratory loss in the effort to retain their turgescence. The stream of water along the course of the water conducting tissues of *Mimosa pudica* must in any case be an extremely active one if turgescence is to be fully maintained under conditions favouring active transpiratory loss, no matter whether the drain upon it be carried on by all the active tissues in like amount or by a certain class of them in excessive amount. In either case the facilities for transpiratory loss remain excessive, and the demand for water to satisfy the osmotic capacities of the tissues is very high, so that turgescence can only be fully maintained under external conditions favouring the occurrence of transpiration by means of a very active current along the course of the water conducting system. Whenever atmospheric conditions are such as to favour transpiration, turgescence can, therefore, be fully maintained at a high level only by means of proportionately active root supply of water, and any sudden increase in transpiratory loss or diminution in root supply must necessarily disturb the pre-existing equilibrium and give rise to a loss in turgescence which will of course, manifest itself most rapidly and readily in those tissues which present the greatest textural facilities for the escape of water. Loss in turgescence originating in any disturbance between the relations of general supply and loss of water will not occur with equal rapidity everywhere, for the rate of loss must be affected on the one hand by the osmotic capacities of the various tissue elements, and on the other by the structural facilities which they provide for the escape of liquid, and where no great difference in osmotic properties is present, those tissues which present the greater structural facilities for the escape of liquid from the interior of their turgescent elements will lose turgescence most rapidly, and with this will become relatively weaker than they previously were. But in the motor organs of *Mimosa pudica*, and especially in those of them which are most subject to rapid movements, we have to deal with opposing masses of tissue which differ very greatly from one another in the textural facilities which they provide for rapid filtrative escape of liquid. Any sudden increase in transpiratory loss or decrease in the activity of root supply must necessarily give rise to decreased liquid pressure throughout the water conducting system generally, and this in its turn to an increased tendency to filtration from the interior of turgid elements. But the rate of filtration in particular elements must be affected by the structural features which they present, and with this corresponding alterations in their relative strength must be established. Where filtrative facilities are present in very different degrees in opposing masses of tissue, as is the case in the primary and tertiary

pulvini of *Mimosa pudica*, very considerable alterations in relative strength must thus be rapidly established and, the equilibrium of position being correspondingly disturbed, movements must occur with proportionate rapidity.

But if all the movements of the leaves of *Mimosa pudica*, apart from those which attend the presence or absence of solar stimulation or other agencies affecting assimilatory activity, owe their origin to such purely physical causes, the readiness and the degree in which they manifest themselves ought certainly to bear some evident relation to the presence or absence of conditions favouring the occurrence of rapid alterations in the relations existing between general loss and supply of fluid, or affecting the activity of processes of local filtration; and there is abundant evidence that such a relation really exists. Its existence is demonstrated by the fact that the occurrence, rate, and extent of movement following the incidence of various disturbing agencies are alike manifestly affected by conditions of telluric and atmospheric humidity. According to Haberlandt's theory, the extent of propagation of movement ought to bear a direct relation to conditions securing excessive root-supply and depressed transpiratory loss;* but in fact the relation, in place of being a direct, is an inverse one. When the soil is saturated and atmospheric humidity excessive, the capacity for movements and the rate and extension with which they occur are alike at a minimum, and it is when the soil is relatively dry and atmospheric humidity low that they attain their maximal development. It would be strange indeed were this not so, seeing that conditions of atmospheric and telluric saturation are calculated to increase the stability of turgescence, whilst aridity of soil and air must inevitably tend to render it unstable. So long as air and soil are alike saturated, there can be nothing to interfere with the tissues fully satisfying any osmotic capacities which they may possess; and consequently, apart from variations in the degree with which they exercise their assimilatory functions, there is nothing to interfere with the continuous maintenance of turgescence at a given standard. All the tissues may not possess osmotic capacity in like degree, but the conditions are such as to allow them all fully to satisfy what capacity they have. There is an entire absence of any struggle between osmotic capacity and any agencies tending to give rise to general loss of water. The only loss of water which is going on is that connected with assimilatory decomposition, and this is amply covered by the excessive root-supply. But when the soil and air are not saturated, the equilibrium of turgescence can only be maintained so long as general supply and loss of water continue to bear a uniform relation to one another. Any rise in loss without corresponding increase in supply must make for decreased turgescence, and any fall in loss without corresponding depression of supply for increased turgescence. A high degree of turgescence may in certain cases coincide with a great capacity for movement, but only when it is maintained in spite of rapid general loss of water; only when it exists as the result of an accurate balance between supply and loss; and therefore we do not find the capacity for movement high in cases where conditions are such as to give rise to diminished transpiration without affecting assimilatory activity and therefore osmotic property.

It would be easy to multiply examples of experimental results showing the truth of the statements contained in the previous paragraph; but in order to avoid breaking the continuity of the text to an inconvenient extent, one or two selected examples alone are introduced here, and the mass of experimental evidence is transferred to the tables which

* Op. cit.

are contained in Appendix E The effects of exposure to the influence of saturated soil and atmosphere in diminishing capacity for movement are constantly presenting themselves in the most conspicuous fashion in various ways Whilst working at the subject I have had constant occasion to take specimens of *Mimosa pudica* from the garden in which they are grown to my laboratory which is situated at a distance of about a mile from it. When the transfer is effected during periods when atmospheric humidity is relatively low, even slight displacement of pot plants is followed by extensive movement of the leaves, and the agitation to which they are exposed during the drive over the rough road which intervenes between the two localities certainly leads to maximal movements in the pinnules and primary petioles, and to considerable convergence of the secondary rachises But with increased humidity the tendency to the occurrence of movement decreases, and when humidity of soil and atmosphere are at a maximum, the plants undergo all the agitation to which the transfer exposes them either without exhibiting any movements at all, or movements of only the most limited and partial kind Parallel phenomena make their appearance under the influence of artificial elevation or depression of atmospheric humidity If two plants luted into carefully stoppered and waxed pots be exposed side by side in two hermetically sealed chambers one containing a vessel of water and the other a vessel of pure sulphuric acid, their leaves are of course coincidently exposed respectively to a saturated and to a very dry atmosphere As the result, transpiratory loss is arrested in the one but rises to a high level in the other, and corresponding differences in their so-called irritability also make their appearance The leaves in the saturated atmosphere become highly elevated and extremely expanded, and after an hour or two of exposure they fail to respond even to the violent agitation produced by shaking the chamber within which they are enclosed The leaves in the sulphuric acid chamber, on the other hand, also show extreme expansion and elevation, but are very susceptible to agitation, even slight shaking of the chamber being followed by depression of the primary petioles and complete assumption of the nocturnal position by the pinnules So, again, when a leaf or a portion of a shoot bearing several leaves is separated from a plant at a time when air and soil are alike relatively dry, the separation is followed by immediate, rapid and complete movements in the pinnules and primary petioles and by considerable convergence of the secondary rachises, whilst when atmospheric and telluric moisture is excessive, no movements whatever manifest themselves for some time, and the movements which ultimately do occur are very slowly, imperfectly, and gradually conducted Under conditions of maximal moisture, the primary absence of any movement whatever, and the delayed and imperfect character of those which ultimately occur, become wonderfully conspicuous Under such circumstances, shoots will frequently stand exposure to all the disturbing influences of separation from the axis, and of considerable and relatively prolonged agitation without showing any appreciable movements I have accordingly been able to separate shoots and transfer them from the site in which they were grown to my laboratory without their showing any more evidences of movement than rooted plants do under conditions of high soil and atmospheric moisture

Under similar circumstances exposure to conditions which determine the artificial escape of liquid from the tissues produce minimal effects as regards movement When the air and soil are both moderately dry, amputation of the tip of a distal pinnule is normally followed by immediate and rapid action in the injured pinnule and simultaneous, or practically simultaneous, action in the opposite one, rapid spreading centripetal

action along the pinnules of the same secondary rachis, convergence of the one or it may be of all the other secondary petioles, rapidly spreading centrifugal action along the course of one, two or all the other secondary rachises, and maximal action in the primary pulvinus leading to the fullest depression of the primary petiole. But when soil and air are alike damper, the extension and rapidity of movements steadily diminish; and when saturation is approached, a minimum of movement is attained except under the action of other factors than mere escape of liquid from the tissues. During periods of excessive moisture the injury to the pinnule produces no immediate movement even locally, gradual exudation appears conspicuously at the site of section, and this is presently followed by slow gradual elevation of the injured pinnule. In some cases no other effect whatever follows; in others, movements are confined to the opposite pinnule, and in still others, very slow and imperfect elevation of a certain number of other pinnules in the distal half or third of the same pinna occurs. Both rate, amount and extension of movement most unequivocally bear an inverse relation to conditions of soil and atmospheric moisture; where soil—and atmospheric moisture are present in maximal degree, the movements following section attain their minimum in regard to rate, amount and extension; where soil and atmospheric moisture reach the lowest level at which they do not lead to permanent assumption of the nocturnal position by the pinnules, the movements following section attain their maximal development.

The same holds good in regard to movements originating in connection with other influences. The movements which follow the application of heat to the tissues are normally more extensive than those following section, but their extent and rapidity are equally affected by the existing conditions of atmospheric and telluric moisture. The application of an open flame to the tip of a distal pinnule of a distal pinna is in hot dry weather followed by immediate action, spreading rapidly over the entire leaf, and in many cases succeeded by action in many more leaves on the same axis both in the centripetal and centrifugal direction. But, where conditions approaching saturation prevail, similar treatment is followed by action which is both of a more gradual character, and which does not extend beyond the pinnules of the directly injured pinna (Appendix D).

The above facts clearly show that the capacity for movements, the rate at which they are conducted, and the extent to which they are propagated, bear a direct relation to the extent to which rapid general loss of liquid can occur; and the question arises is whether this is to be regarded as indicating increased irritability and contractibility in the protoplasts of the motor organs under the influence of conditions favouring general loss of liquid from the tissues, or as evidence that the movements are dependent on losses in turgescence directly connected with the loss of liquid itself. Now, there is no independent evidence that conditions of atmospheric humidity are capable of acting directly upon the irritable and contractible functions of the protoplasts of the motor organs—no evidence to show that the irritable and contractible functions are stimulated by a dry atmosphere and depressed by a moist one. But there is abundant independent evidence to show that conditions of atmospheric humidity directly affect turgescence owing to the effects which they produce on transpiratory loss, and there is satisfactory structural evidence that the opposed masses of tissue within the motor organs are liable to undergo losses in turgescence in unlike degree, and at unlike

rates, under the influence of increased transpiratory loss The only logical conclusion therefore which can be arrived at from the data is, that the differences in the phenomena of movement presenting themselves under the influence of different conditions of atmospheric humidity are owing to corresponding differences in the degree to which these conditions favour the occurrence of purely physical loss of water from the tissues The phenomena are readily explicable on the theory that the movements have a purely physical origin, they remain entirely mysterious on that which regards them as the result of active protoplasmic contraction.

But another phenomenon frequently manifests itself in connection with the presence of excessive atmospheric humidity which is even more inexplicable on the theory of active protoplasmic contraction In cases in which not only both air and soil are saturated with moisture, but recent rainfall has occurred and loaded many of the leaves with adherent drops of water, phenomena which according to the contraction theory must be regarded as indicative of special irritability of the primary pulvini, frequently manifest themselves In such cases, after amputation of the tip of one of the distal pinnules, either no movement at all occurs in the pinnules, or slow imperfect movements occur in the injured pinnule alone, or in it and in one or two neighbouring ones, and yet rapid and profound depression of the primary petiole takes place shortly after the injury and often before any pinnular displacement has begun to appear (*vide* Appendix A) On the theory that movements are due to active protoplasmic contraction, this must be taken to indicate that excessive atmospheric humidity decreases the irritability and contractility of the tertiary pulvini, and increases those of the primary one, that is, that the same cause gives rise to different effects in two parallel sets of organs But this is a conclusion for which no evidence exists save the very phenomenon for which it has to serve as an explanation But on the physical theory there is nothing remarkable about the coincidence We know, that under any circumstances, the mass of tissue in the primary pulvinus which makes for elevation of the primary petiole has to struggle, not only with its local opponent, but also with the depressant action of distal leverage, and it is clear that any accumulation of raindrops on the pinnæ must increase the latter But adherent rain drops cannot serve to increase the resistance which has to be overcome by the tissues in the tertiary pulvini which make for depression of the pinnules, and as a rule they must tell directly against their elevation In the primary pulvini the masses of tissue which make for depression, and which are structurally stronger than their opponents, are co operated with by the adherent rain drops in the attempt to depress the primary petiole, in the tertiary pulvini the structurally feebler tissues, instead of encountering any additional opposition under the circumstances, are aided in securing depression of the pinnules That is, under the circumstances, the tissues which make for the diurnal position are relatively weakened in the primary pulvini and relatively strengthened in the tertiary ones, or, in other words, under the circumstances, the stability of the equilibrium of position is decreased in the primary pulvini and increased in the tertiary ones But, if this be so, a fall in general fluid pressure incident on the escape of liquid from the tissues of an injured pinnule, and which is incapable of producing any but very limited effects in the site of increased stability, may readily induce considerable effects in that of decreased stability So far as transpiratory loss is concerned, both primary and tertiary pulvini are, under the circumstances, in a

condition of relatively stable equilibrium; but in the case of the primary pulvinus this is discounted by the coincident increase in distal leverage, whereas in the tertiary pulvini it is either not interfered with or positively strengthened. It can be no wonder, then, that a disturbing factor should be capable of giving rise to effects differing in degree within the two areas.

Phenomena of a like nature often manifest themselves in plants which are suddenly transferred from a saturated atmosphere to one of the same temperature, but considerably drier. Under exposure to the influence of an artificially saturated atmosphere in a moist chamber, if sufficient illumination be provided, the pinnules and secondary rachises of the leaves assume their maximal diurnal position of extreme expansion. But the primary petioles, in place of tending to sink as they do under natural diurnal conditions, become highly elevated. All parts of the leaf at the same time pass into a condition of abnormally stable equilibrium, so that, as a rule, no movements follow comparatively violent agitation. But, if the cover of the chamber be suddenly and gently withdrawn so that the tissues are exposed to a relatively dry atmosphere, movements occur after a brief interval. These, however, are frequently confined to the primary petioles, which undergo rapid and deep depression, and it is only occasionally that any conspicuous rapid elevation of the pinnules manifests itself. On the theory that movements are essentially due to active contraction of the protoplasts of the motor organs, these phenomena must be taken to indicate that transfer from a saturated to a relatively dry atmosphere causes protoplasmic stimulation more readily in the protoplasts of the primary pulvini than in those of the tertiary ones. But on the physical theory no such arbitrary assumption is called for. When the distal portions of the leaves are saturated with moisture and have been continuously exposed to conditions favouring active assimilation, their weight must attain its maximal development, and with this the strain upon the primary pulvinus must be proportionately increased. Even in the absence of saturation, prolonged exposure to conditions favouring assimilation causes sufficient increase in leverage to aid materially in inducing a depression of the leaves from their late nocturnal position of extreme elevation; but when transpiratory loss is absent, it is unable to cause depression in spite of the aid which mere excess of distal fluid must yield to it. The strain, however, upon the primary pulvinus in maintaining erection must be very great, and when the plant is suddenly exposed to conditions implying an abrupt onset of transpiratory loss disturbing the pre-existent condition of liquid equilibrium, the effect naturally manifests itself most readily in it as the weakest part in the motor apparatus. Where the atmospheric conditions are such as to give rise to transpiratory loss in limited degree only, the disturbance tells only on the weakest part of the apparatus, and depression of the primary petioles occurs; where the loss is greater, movements occur in the pinnules, but the loss must be very excessive to induce any appreciable movements of convergence in the pinnæ, because in the secondary pulvini conditions favouring a rapid loss in turgescence are present in much lower degree than they are in the other motor organs.

The extent, rapidity and propagation of movements are then unequivocally related directly to the presence of conditions in the environment regulating general supply and loss of water. But if disturbances of the equilibrium between supply and loss be the essential factor which determines all movements not dependent on alterations in turgescence connected with fluctuations in solar stimulation and assimilatory activity, movements

ought to occur in connection with exposure to any conditions implying considerable disturbance of pre existing relations between supply and loss, and these ought to be rapidly carried out where the conditions are such as to imply rapid disturbance It is easy to acquire evidence that this theoretical requirement is amply met by actual facts The phenomena which have just been described as arising in connection with the transfer of plants from saturated to relatively dry air are, of course, an example of movements originating under such conditions, and one has not to look far for others of a similar nature It has already been pointed out that when plants which have been for some time in the shade, and whose pinnules have attained a maximal degree of expansion are exposed to strong, direct sunshine, either as the result of the natural diurnal alterations in distribution of the latter, or of transfer from one locality to another, gradual movements of elevation and convergence set in in the pinnules, so that the leaves presently become much less fully expanded than they previously were If atmospheric humidity be very low and the soil very dry, the movements are continued until the pinnules have assumed their maximal nocturnal position If, on the other hand atmospheric and telluric aridity be not very great, the displacement is only a partial one, but it is always sufficient to cause the appearance of insolated plants to differ strikingly from shaded ones in their immediate vicinity Where atmospheric and telluric humidity are alike moderate the activity of root supply is incapable of maintaining active turgescence in the tertiary pulvini at the same level as when transpiratory loss was considerably less, but it is capable of maintaining enough turgescence to prevent the pinnules from passing on into the fully developed nocturnal position But when atmospheric humidity falls very low, and when the supply of water in the soil is very small, the disproportion between root supply and transpiratory loss becomes excessive, and the movements are carried out in maximal degree The phenomena are precisely parallel to those occurring in the case of other nyctitropic leaves under similar circumstances, but the movements are more readily induced and more rapidly conducted than they are in these because of the exceptional facilities for transpiratory loss and for rapid redistribution of liquid which the tissues of the leaves present Parallel phenomena of exceptionally rapid manifestation of the effects of increased transpiratory loss manifest themselves in connection with certain non nyctitropic leaves An exposure to strong, direct sunshine, as brief or almost as brief as that sufficing to give rise to sensible elevation of the pinnules of *Mimosa pudica* will induce perceptible general wilting in the leaves of certain aroids, such as "*Pothos violacea*' of gardeners unless both soil and air are loaded with moisture In the case of "*Pothos violacea*' we have evidence of general and evenly diffused loss in turgescence, in that of *Mimosa pudica* of specially localised loss in turgescence as the result of exposure to increased transpiratory loss, and in both cases cases alike the loss in turgescence is exceptionally rapid No one would dream of ascribing the wilting of the leaves of "*Pothos violacea*" to active contraction of the protoplasts of the tissues, but the firmly fixed belief in the existence of special functional endowments in the protoplasts of the motor organs of *Mimosa pudica* might lead to a belief that the parallel phenomena of the movement of the pinnules was owing to some directly stimulant action of the sun's rays, were it not that precisely similar ones manifest themselves where increased transpiratory loss arises quite independently of any alterations in conditions of illumination, and that the results following exposure to direct sunshine vary in degree with the extent to which facilities for transpiratory loss are present

If two plants of *Mimosa pudica* be exposed side by side to strong direct sunshine, the one being included in a moist chamber and the other in a sulphuric acid chamber* the pinnules of the former will remain nearly fully expanded, but those of the latter will pass into the maximal nocturnal position. When exposed to diffuse light, on the contrary, the pinnules in both cases alike (granting of course that sufficient soil moisture is supplied to the plant whose leaves are exposed to a dessicated atmosphere), attain a maximal degree of expansion. The displacement which occurs in the leaves in the moist chamber under exposure to direct sunshine may be fairly credited to the onset of a certain amount of transpiratory loss, for, as the exposure implies continous elevation of temperature within the chamber, absolute atmospheric saturation cannot be present within it. In so far as illumination and temperature go, the two plants are exposed to precisely like conditions, and yet the pinnules undergo only slight displacement in the one case and complete displacement in the other, thus leaving the differences in transpiratory loss as the only factor accounting for the differences in the result of exposure in the two cases.

In cases like the above, movements occur under the influence of the increased transpiratory loss incident on exposure to the sun's rays, but equally considerable movements attend excessive transpiration caused by other means. If a pot-plant of *Mimosa pudica* in which the leaves are in the normal diurnal condition be transferred from a relatively cool and moist atmosphere to one which is considerably warmer and very dry, the pinnules gradually assume the fully developed nocturnal position, although the conditions of illumination to which they are exposed remain precisely as they were before. Very little, if any, perceptible displacement occurs in the secondary rachises, but the primary petiole becomes extremely elevated. Here certainly no stimulant action of the sun's rays can come into play as the determinant of the movements, and as we find the latter manifesting themselves at temperatures under which the diurnal position is fully maintained so long as the air is humid, the only thing which is left to account for them is the excessive transpiratory loss to which the tissues are exposed. It is, of course, possible to assume that excessive transpiratory loss gives rise to active protoplasmic contraction; but there is no evidence whatever that it actually is so, and there is no question that it does give rise to loss in turgescence from purely physical causes. The rate of movement of the pinnules varies with the temperature of the air and, where this very considerably exceeds that of the atmosphere to which the plant was previously exposed, sudden rapid movements may occur in a certain number of them, accompanied occasionally by sudden depression of the primary petiole. But a still more remarkable phenomenon normally follows the removal of the plant from the artificially warm and dry atmosphere to that to which it has been exposed (*vide* Appendix E). If a plant be retransferred to its original environment at a time when its pinnules have only partially assumed the nocturnal position and every care being taken to avoid any mechanical agitation, no farther movements of elevation take place in the pinnules, but, after a brief pause, all or a majority of the primary petioles become suddenly and rapidly depressed. Now, this is a sequence of events which is utterly unexplicable on the theory that the movements

* In all cases in which exposure in a sulphuric acid chamber is mentioned, it is assumed that effectual means, similar to those described on page 77, were taken to secure that the only additions to atmospheric humidity were derived from transpiration.

are essentially dependent on active stimulation and contraction of the protoplasts of the motor organs, unless indeed on the groundless assumption that exposure to hot and dry air acts as a specific stimulant of the protoplasts of the motor organs of the tertiary pulvini and exposure to cool, moist air as a specific stimulant to those of the primary ones But if we accept the theory that the movements are dependent on conditions affecting supply and loss of fluid, the sequence admits of ready explanation Sudden transfer to a relatively warm and dry atmosphere must give rise to increased transpiratory loss and must establish a drain upon all the turgescent elements of the tissues to which they were not previouly exposed, so that, unless root supply sustains an equivalent increase, a general loss of turgescence must tend to be established The actual loss in turgescence which will occur in individual masses of tissue will be rapid and extensive in direct relation to the facilities which they provide for the escape of liquid from the interior of the cell elements of which they are composed But the tissue elements in those masses of tissue which make for the diurnal position in the primary and tertiary pulvini afford much greater facilities for the escape of liquid, than those which make for the nocturnal position Hence a relative weakening of the former must occur, and with this, if no interfering factor come in to modify the result, movements towards the nocturnal position must necessarily ensue In the case of the tertiary pulvini, nothing comes in to interfere with the execution of such movements, and they are accordingly carried out at rates varying with the rapidity at which the weakening loss in turgescence occurs within the pulvinar tissues making for the diurnal position But, in the primary pulvini, the local weakening is accompanied by coincident rapid decrease in distal leverage which discounts and more than discounts it The mass of tissue in the primary pulvinus which makes for elevation of the petiole is weakened in so far as respects its local pulvinar opponent, but is strengthened in respect to the total resistance which it has to overcome, and hence elevation and not depression occurs But when the plant is once more suddenly transferred to its originally cool and moist environment, a sudden check is put on the activity of transpiratory loss, and with this no farther elevation of the pinnules occurs, and distal leverage in place of undergoing any farther decrease begins to increase Simultaneously another important factor affecting the general distribution of fluids throughout the tissues comes into play The rapid cooling following transfer to the cool air necessarily implies rapid contraction in all the gaseous contents of the water conducting tissues, and this must tend to give rise to a back draught on the liquid contained within the actively turgescent ones and, therefore to enhance filtrative loss from them Ordinarily the effect of this on the pinnules is done away with by the coincident cessation of active transpiration, and, consequently as a rule, no appreciable movement occurs in them, but in the case of the primary pulvinus nothing comes in to interfere with its action The cessation of transpiratory loss does not here tell against the occurrence of movement, but directly in its favour in consequence of the increase in distal leverage which it necessarily involves, and, consequently, depression of the primary petioles naturally tends to occur As will be presently demonstrated, a sudden expansion of the gaseous contents of the water conducting tissues may also serve to occasion sudden movements, apparently as the result of the obstruction to onward flow of water which it induces if pushed beyond certain limits, but any obstruction which arises in cases like the above on the introduction of the plant into the heated atmosphere is, unless it be present in very high degree, unable to determine

the depression of the primary petiole in consequence of the coincident rapid diminut in distal leverage which is present.

It has already been pointed out that very brief exposure to the direct rays of sun is sufficient to give rise to slow, progressive movements of elevation of the pinnu which, under certain conditions of soil and atmosphere, may ultimately lead to a assumption of the nocturnal position; but in certain cases the rate of movement may so much accelerated that the progress of elevation and convergence becomes visible the unaided eye, or even as rapid as it is in cases where the leaves are exposec the influence of any of the common so-called stimuli. When leaves are gently detac from the axis, elevation of the pinnules and a certain amount of convergence of secondary rachises usually occurs. The extent and the rate of movement, however, v greatly under different circumstances, more or less complete suppression occurring connection with the presence of excessive humidity, whilst, when soil and air alike very dry, the movements of the pinnules are immediate and complete, and convergence of the secondary rachises considerable. Supposing that the process separation be effected in the early morning, ere the leaves have been exposed to di sunshine, and at a time when atmospheric and telluric conditions of moisture are mean, the pinnules as a rule all assume the maximal nocturnal position within a l period, but the secondary rachises exhibit little or no appreciable movement. If the leaf, having been gently laid down on a glass plate and covered with a bell glas protect it from mechanical disturbance, be exposed to diffused sunlight, the pinn will gradually resume the diurnal position more or less completely, and will retain it a very considerable period ere slow insensible elevation sets in. Should the appar however, be exposed to direct sunlight after expansion has occurred, and the bell be gently removed, movements very soon make their appearance. Where atmospheric telluric moisture are both excessive, or the sunshine is veiled and comparatively fe the movements are often merely of the slow, insensibly progressive character of t occurring in leaves attached to the axis when exposed to direct sunshine; but when ditions of humidity are not so high, or the sunshine is stronger, they occur in increa degrees of rapidity until, in many cases, rapid and complete elevation of the pinn and convergence of the secondary rachises take place in precisely the same fashic they do after sudden concussion, incision of the tissues, or application of strong Where movements of this sudden, rapid type have occurred, the assumption of nocturnal position is not however permanent; but, unless the air be very dry succeeded by a partial recovery of the diurnal one preceding the occurrence of slow progressive movements of elevation. Where, on the other hand, the moven have been throughout of a slow, insensible character, continued exposure gives rise t interruption in their progress.

Now, these phenomena can hardly be accounted for satisfactorily on the theory the movements, and, especially the rapidly executed movements, of the leaves are de dent on the occurrence of stimulation and active contraction of the motor organs. movements in many cases present all the characters of those following the action c called stimuli, being as abrupt, as complete and as spreading as any of these are, according to the theory, they must, therefore, be regarded as owing to the occur of stimulation attending exposure to direct sunshine. But if this be so, how do happen that, so long as leaves retain their normal relation to the axis, exposu

direct sunshine normally occasions only slow insensibly progressive movements Why should exposure to the sun's rays only give rise to movements which, judging from the parallel phenomena occurring in non motile leaves under similar circumstances, are unequivocally dependent purely on increased transpiratory loss, so long as the leaves retain their normal connection with the axis, and to movements dependent on active protoplasmic contraction when they no longer do so? This, moreover, is not the only problem which has to be accounted for, for, if exposure to the sun's rays primarily occasions active contraction of the protoplasts of the motor organs, why should it cease to do so? why should continued exposure be accompanied by partial recovery of the diurnal position? These are questions which the theory apparently can answer only by means of a series of arbitrary assumptions

But if this theory be incapable of accounting for the phenomena, can that which ascribes the occurrence of rapid movements to purely physical causes do so any more satisfactorily? When a leaf is suddenly detached from the axis, an abrupt arrest is of course in any case put to any further root supply of water But in *Mimosa pudica* owing to the high liquid tension throughout the tissues, this is accompanied by active exudative discharge of a relatively large mass of liquid from the extremity of that portion of the petiole which remains attached to the distal portion of the leaf The liquid which escapes may be mainly derived from particular tissues or it may not, but in any case, the effect must be a general loss in liquid tension throughout the entire leaf, and consequently a tendency to increased drain upon the active tissues In cases where the tissues are excessively saturated as the result of antecedent conditions of atmospheric and telluric humidity, and where at the time of separation from the axis transpiratory loss is very low, the intrinsic water conducting tissues contain an amount of fluid more or less completely sufficient to make good the actual discharge of liquid attending separation, and, for the time being, the arrest in root supply, and hence either no movements at all occur, or any which do occur are slight and partial With any diminution in the amount of store water, or any increase in the activity of transpiratory loss, the conditions providing for the occurrence of movement will be present in progressively increasing degree, and a point must eventually be reached at which separation from the axis implies immediate active drain upon the turgid elements of the motor organs But this drain will naturally tell most heavily and rapidly on those masses of tissue presenting the greatest filtrative facilities and, therefore, on those which make for the diurnal position, and hence movements corresponding to a weakening of these will occur The masses of tissue in the tertiary pulvini which make for the diurnal position of the pinnules afford great structural facilities for rapid filtration, both from their inherent delicacy and from the great excess of structural strength in their opponents, and hence the pinnules tend to pass on rapidly into the nocturnal position In the secondary pulvini the opposing masses of tissue do not present nearly such considerable differences, and hence movements in the secondary rachises are often almost or entirely absent when the pinnules exhibit conspicuous movement, and under normal circumstances they never exhibit the same activity as those of the pinnules do If transpiratory loss be very active, any liquid which escapes from the turgid pulvinar tissues on the sudden disturbance of equilibrium of general fluid pressure on separation from the axis and any store of water within the water conducting tissues will be rapidly removed and the nocturnal position of the pinnules will remain permanent, and hence no phenomena of recovery of the diurnal position manifest themselves in leaves which are detached from the axis

in very dry hot weather, even if they be subsequently kept in the shade, or in those detached in cooler and damper weather when exposed to strong direct sunshine after separation. But if transpiratory loss be slight, the tissues will retain a considerable amount of water, especially where atmospheric and telluric humidity have antecedently been high for some time, and this, of course, is available to satisfy the osmotic capacities of the active tissue elements to a greater or less extent. Mere separation from the axis has in no way affected the functional properties of the active tissue elements remote from the site of section, it has only removed them from all connection with root-supply of water; and, so long as the inherent water-conducting system retains a sufficient quantity of water, this is of no importance. Whilst the water-conducting system contains a sufficient store of inherent water, it plays the same part to the active tissues that a moist soil does to a plant as a whole. The tissues in the tertiary pulvini which make for the diurnal position are functionally much stronger than their opponents, and hence under continued stimulation by light will undergo a greater increase in osmotic capacity than the latter, and as they also present greater structural facilities for absorption, will appropriate a correspondingly large share of the store of water remaining at disposal. With this they will increase in strength, and a reversion of the pinnules towards the diurnal position must follow. But if, when this reversion has been fairly established, the leaf be suddenly exposed to direct sunshine, a sudden rise in transpiratory loss of water must at once ensue, and with this a renewed drain upon the tissues, leading as before to special weakening of those portions of the pulvini which make for the diurnal position. If the activity of transpiratory loss does not exceed a certain limit, and if the amount of reserve fluid in the water-conducting system be high, this will merely lead to slow, progressive alterations in position of the pinnules, like that which occurs in leaves still attached to the axis when exposed to strong sunshine. But if transpiratory loss be very rapid, and the reserve of water within the water-conducting tissues have been more or less exhausted in supplying the osmotic demands of the actively turgescent tissues, a sufficiently rapid draught may be established to give rise to the occurrence of rapid resumption of the nocturnal position. Subsequently, under continued solar stimulation, a renewed struggle for any remaining reserve-water sets in, and a tendency to recovery manifests itself in greater or less degree, never, however, leading to anything beyond very partial resumption of the diurnal position because of the limited amount of water which is available. Finally, as transpiration continues, the conditions for active turgescence are gradually diminished, and ultimately abolished, and with this the various parts of the leaf permanently assume the positions which are determined by their passive structural peculiarities.

During continuous periods of fine, settled weather the phenomena attending separation of leaves from the axis show regular and conspicuous differences, according to the time of day at which the experiment is conducted. The effects of primary separation from the axis and of subsequent exposure to diffuse and direct sunshine are not alike in the early morning and in the afternoon. When leaves are separated in the morning, ere the dew has evaporated, and whilst the air is relatively humid, the extent and rate of primary assumption of the nocturnal position by the pinnules is less than it is in the afternoon, the amount of primary recovery is greater, the tendency to the occurrence of rapid movement on exposure to direct sunshine is less; secondary partial recovery from the nocturnal position after rapid movements constantly occurs in greater or less

degree, and the secondary rachises throughout exhibit little or no movement In the afternoon the pinnules assume the nocturnal position much more rapidly and completely, primary recovery is much more limited, rapid resumption of the nocturnal position on exposure to direct sunshine occurs more frequently and much more completely, secondary recovery does not follow continued exposure, and the secondary rachises exhibit more rapid and much more considerable movements of convergence

In order to explain these experimental results on the ordinarily accepted theory of the causation of the movements in *Mimosa pudica,* it must be assumed either that separation from the axis and exposure to the sun's rays are stronger stimuli to protoplasmic contraction in the afternoon than in the morning or that the protoplasts are more irritable in the afternoon than in the morning, that separation from the axis render the contractile protoplasts more irritable or more contractile than they are whilst retaining their normal relation to it, that exposure to direct sunshine is in the morning, only a temporary stimulant to contraction but in the afternoon a permanent one and, finally, that the protoplasts of the tertiary pulvini are much more irritable than those of the secondary ones But any such assumptions have absolutely no foundation beyond the belief that the movements must be dependent on active contraction of the protoplasts of the motor organs, and some of them are directly controverted by facts Separation from the axis and exposure to the sun's rays produce *less* effect in the afternoon than in the morning if the air and soil, in place of having become dryer in the interval, have become more humid, and leaves or shoots separated from the axi when the soil and air are alike excessively humid are much *less* "irritable" than leaves or shoots attached to the axis when soil and air are both very dry

The other theory can, at all events point to the existence of differences in the state of the tissues and of the environment corresponding with the differences in the phenomena of movement at different periods So far as the tissues are concerned, it is evident that in the morning they must normally contain a greater bulk of fluid than they do in the afternoon They have not had time to lose much by transpiratory loss owing to the relatively high humidity actually prevailing at the time and they have previously been exposed to a prolonged period of abolished transpiration Under these circumstances they are likely to contain a considerable excess of water within the water conducting system beyond the bulk which is absolutely necessary to maintain active turgescence under the existing conditions of immediate transpiratory loss The amount of surplus will, of course, vary very considerably under different circumstances, but where the humidity of the soil is relatively high, it may well attain such a level as to suffice, in coincidence with slight transpiratory loss to maintain turgescence in the active tissues for some time after a complete arrest is put on any further root supply by separation from the axis, and even in spite of actual active discharge of water attending the latter Under such circumstances there is no immediate local demand for root supply, as the local water conducting system has become a reservoir for a greater bulk of water than is immediately required to make good transpiratory expenditure It is not then at all surprising to find that, where previous and existent conditions of soil and air imply excessive supply and minimised loss of water separation from the axis is attended either by an entire absence of movement, or by very feeble and limited movement only Where the water content is such that the active escape of liquid is sufficient to give rise to a considerable fall in the liquid tension present throughout the water conducting system directly, or primarily throughout

the system of sieve-tubes in the bast, as Haberlandt maintains, this may well give rise to sudden increase in the amount of filtration occurring from the actively turgescent tissues of the motor organs. When the pulvinar tissues which make for the diurnal position afford much greater facilities for filtration than those which make for the nocturnal one, they must, under the circumstances, rapidly become relatively weakened, and consequently rapid movements of elevation and convergence of the pinnules must be liable to occur. The liability to the occurrence of rapid movement must vary directly with the degree to which the opposing pulvinar masses differ from one another in respect to the filtrative facilities which they present, as it is on the presence of such differences that alterations in their relative strength are, under such circumstances, determined, and hence movements are much less constant and conspicuous in the secondary rachises than they are in the pinnules. But, so long as transpiratory loss remains low, such filtrative escape does not imply absolute loss of liquid; it merely implies the displacement of a certain amount of liquid from the interior of the actively turgescent elements of the motor organs. A local supply of liquid will thus remain available for expenditure in the re-establishment of active turgescence, the precise amount varying, of course, with the amount of reserve liquid originally present and with the activity of transpiratory loss for the time being. Consequently, under the influence of continued exposure to photic stimulation and low transpiratory loss, turgescence must tend to be more or less completely re-established, seeing that nothing has happened to interfere with the assimilatory activity of the tissues of the motor organs, and that a supply of water is present to meet the increased osmotic capacity of the cell-sap connected with continued assimilation. But as the masses of pulvinar tissue which afford the major facilities for filtrative loss are also those which under the influence of light undergo the greatest increase in turgescence, continued exposure must lead to their gradually regaining their relative strength to a greater or less degree, and with this a resumption of the diurnal position must be correspondingly established according to the available supply of water. A new position of unstable equilibrium is thus attained, and may remain unaltered for a considerable period so long as external conditions remain the same. But if the leaves be now suddenly exposed to the direct rays of the sun, they are placed under conditions which imply increased transpiratory loss. If the increase be a very limited but progressive one, as it is on very damp mornings or when the sunshine is feeble, the effects which it will produce will be delayed, and when established will be of a slowly progressive character: the position which had arisen under the previous conditions will no longer be maintained, but the departure from it will not begin for some time and, when fairly established, will be of an insensibly progressive character, because the transpiratory loss which causes it is a very gradual one. In any case the drain will tell most heavily on those tissues which present the greatest structural facilities for escape of fluid, and, consequently, the initial effect of exposure to direct sunshine is the establishment of movements towards the nocturnal position. But where exposure implies the establishment of sudden and great increase in transpiratory loss, the movements may no longer be of a slow and insensibly progressive character, but may be conducted as rapidly, or almost as rapidly, as those attending the original separation of the leaf from the axis. The sudden and great increase in transpiratory loss here plays the same part as the active discharge of fluid from the detached petioles in giving rise to a considerable fall in liquid tension, and, with this, sudden and excessive drain upon those masses of pulvinar tissues

which afford special facilities for filtrative escape of fluid Under continued exposure, however, an assimilatory struggle for the remaining supply of water is once more established, and the tissues making for the diurnal position once more undergo a relative increase in strength This for some time enables them to give rise to a partial resumption of the diurnal position even under the new conditions of transpiratory loss, but, as the latter continues, they again become weakened, and the various parts of the leaf gradually and finally assume the positions corresponding to the passive structural strength of the various tissues entering into their composition

In the afternoon of the same day, supposing that it has been one of continuous sunshine, and that no special interfering factors have come into play, the conditions both of the tissues themselves and of their environment are very different from what they were in the early morning The tissues have for so long been exposed to active transpiratory loss as to ensure a great diminution, if not a total expenditure, of any surplus of water content beyond the amount necessary to meet the immediate demands of the active elements, and atmospheric conditions are such as to imply much more active transpiratory loss than that which was present in the morning Under the circumstances, it is only natural that any phenomena of movement dependent on alterations in the relations of supply and loss of water should show certain modifications in character, and that these modifications should be of the nature of those which are actually present The supply of reserve-water within the water conducting system being greatly decreased or practically exhausted, and transpiratory loss being greatly increased, the maintenance of the diurnal position is secured only by means of immediate expenditure of the water furnished by the stream traversing the water conducting system from the roots, and hence separation from the axis implies an immediate and very considerable drain upon the active tissues This secures proportionately rapid and complete action in the pinnules and considerable movement in the secondary rachises Under such circumstances the recovery of the diurnal position is naturally less complete exposure to direct sunshine is followed by more rapid movements and more frequently by abrupt, spreading movements, and the secondary assumption of the nocturnal position is not only much more complete than it was in the morning, but is also final and is never succeeded by any symptoms of secondary recovery.

In dealing with these phenomena of movements in leaves and shoots when separated from the axis and deprived of root supply of water, it has been pointed out that exposure to direct sunshine does not normally give rise to abrupt, but only to insensibly progressive movements The exposure necessarily implies just as much increased transpiratory loss as it does in the case of detached leaves and yet the occurrence of sudden movements is quite exceptional in place of being a frequent or, under certain circumstances a constant event, as it is in the latter This is readily explicable on account of the fact that leaves whilst they are attached to the axis are not solely dependent on inherent water supply, but are permanently practically in a condition parallel to detached leaves containing a large amount of reserve water The continuous supply of water ascending from the roots replaces the local reserve of water in detached leaves in which only slow insensibly progressive movements occur. In neither case is there any normal tendency to rapid, sudden movements, because the sudden increase in transpiratory loss is to a great extent equilibrated by the presence of an ample supply of water The sudden increase renders the maintenance of the maximal diurnal position impossible, but the loss in

scence is a gradual one, and where root-supply is abundant and atmospheric humid- s not excessively depressed, a modified diurnal position is shortly arrived at, the se nature of which varies with the relations between supply and loss of water, the ences in osmotic properties of the opposed masses of pulvinar tissues, and any altera- in the leverage of distal parts which may have been induced. The reserve-water, ne water continuously supplied from the roots, acts as a kind of buffer interposed een transpiratory loss and the water of turgescence contained within the active es. The increased transpiratory loss must, of course, eventually tell on the amount ater available for the up-keep of turgescence in all cases where root-supply is absent, incapable of increasing in activity to the extent of entirely discounting the increased but in the presence of a large stock of reserve-water or of active root-supply it does so gradually, whereas in the cases of detached leaves, unprovided with much ve-water, an active drain sets in at once upon the turgescent tissues, and specially hose which provide the greatest structural facilities for the redistribution of liquids.

But in certain cases rapid sudden movements do attend the sudden exposure of hed leaves to direct sunshine. In hot dry weather, it not unfrequently happens that n the direct sunshine first strikes upon a plant in the morning a certain number of youngest mobile leaves, in which full expansion of the pinnules has not yet been lished, presently show rapid movements of depression in their primary petioles. The ements in such cases may be owing to the action of the same cause as that which sions sudden movements in detached leaves. They may be owing simply to the en increase in transpiratory drain, acting upon the pulvinar tissues which make the diurnal position at a time when they are specially structurally weak owing to incomplete development; but it appears probable that, in part at all events, they their origin to the action of another factor. The delicate tissues of the terminal ions of the axis on which the youngest leaves are situated are, of course, very readily cted throughout by sudden changes in temperature, and just as a sudden and con- rable fall in temperature must tend to establish a back-draught of liquid into the er-conducting system, so a sudden and considerable elevation may lead to tem- ry obstruction to its onward progress. Any sudden elevation of temperature must sion corresponding expansion in all the gaseous contents of the water-conducting em, and if the expansion exceed certain limits, it must almost inevitably lead to e or less obstruction of the current of water ascending from the roots. It is not, ever, necessary to remain contented with theoretical considerations, for there is clusive experimental evidence which demonstrates not only the occurrence of such ruction, but also the fact that it is amply sufficient to give rise to the occurrence of den and extensively propagated movements. If an open flame, or the points of a ted pair of forceps, be applied to any point in the course of an axis of *Mimosa ica*, or, still better, if the sun's rays be accurately focussed upon it, very conspicuous nomena of movement presently manifest themselves in the leaves, unless under condi- ns of excessive saturation of the soil and atmosphere. In the case of young, soft ots the treatment gives rise to conspicuous local change in colour and to more or less spicuous discharge of liquid upon the surface, but in mature, hard shoots little change colour occurs unless actual charring of the tissues be effected, and there is no exuda- n on the surface. These differences are satisfactorily explained by the differences in nature of the tissues in the two cases. In the young shoots a delicate epidermis vided with stomatic orifices is present covering a mass of young active hypodermal

tissue, whilst, in the mature axis, epidermis has been replaced by strata of corky tissue protecting the deeper portions of hypoderma with a dense impermeable coat, and there is no system of great intercellular channels, like that in the hypoderma of the petioles, to afford accommodation to fluids escaping from the interior of the tissue elements (Plate V, Figs 8, 15) The phenomena are the parallels of those occurring in cases of exposure of shoots to the action of chloroform vapour in which superficial exudation of liquid occurs in young, green shoots and is entirely absent in mature, woody ones Running parallel with these differences in local effects, we find differences in respect to the phenomena of movement following the treatment In the case of the young, soft shoots movements may occur both centripetally and centrifugally along the course of the axis, just as they occur both centrifugally and centripetally after the application of heat to points in the course of petioles, but in old, woody shoots they occur in centrifugal direction alone, unless the point at which heat is applied be immediately in the neighbourhood of the first leaf in the centripetal direction in which case movements may occur in it, but in it alone in that direction (*vide* appendix F)

Now, it is not easy to account for these phenomena of distribution of movement in mature shoots, save as the result of local obstruction to water supply Where the shoots are still young and soft, heating leads, not merely to sudden local expansion of the gaseous contents of the tissues, but to a sudden loss of water of turgescence from the outer surface, precisely similar to that attending immersion in boiling water or death due to exposure to the vapour of chloroform, and in the case of petioles, although any free escape of liquid of turgescence does not occur on the outer surface, ample accommodation for such liquid is afforded by the great hypodermal, intercellular channels but in the hard dense tissues of old axes the suberous strata prevent superficial exudation, and the density of the texture throughout the hypoderma affords no space for any appreciable bulk of liquid save within the interior of the cells, and hence any sudden rise in temperature is practically expended in giving rise to corresponding expansion of the gaseous contents of the water conducting system Where any appreciable exudative discharge of liquid of turgescence takes place as in the case of young soft shoots, two factors affecting water supply come into play, there is both sudden expansion of the gaseous contents of the water conducting system, and a sudden establishment of an abnormal local drain of liquid Any obstructive action of the former can only tell in interfering with water supply in a centrifugal direction unless in the immediate neighbourhood of the site in which it originates, but the abnormal local drain attending exudation must, of course be capable of telling both centrifugally and centripetally. There are thus reasons why movements depending on sudden depressive alterations in water supply should in such cases make their appearance in both directions But where, as in old shoots, no local exudation occurs, where no local drain is established, we have to deal with obstruction alone which can only tell centrifugally, or, in extremely localised fashion, centripetally, and consequently, it is only centrifugally, or, in the immediate neighbourhood of the site of origination, centripetally, that any movements connected with sudden diminution of water supply will occur. Where local obstruction and drain coincide, movements related to defective supply of water may occur in both directions, where obstruction alone is present, they can only occur centrifugally or in the immediate neighbourhood of the site in which the obstruction originates, because everywhere beyond this area in the centripetal direction

the conditions are such as necessarily to imply increased in place of decreased water-supply. No theory of the communication of impulses giving rise to active protoplasmic contraction in the motor organs will account for these phenomena, because none of them can account for the fact that the propagation of movement should, in the case of young shoots, occur in both directions and in that of old ones in one only, or should, at all events, not extend beyond the immediate neighbourhood of the site of application, or, in other words, be confined solely to the area in which obstruction can come into play in inducing decreased supply of water. The theory of active protoplasmic contraction here once more breaks down, whilst the physical theory is able to afford a satisfactory explanation.

The phenomena of distribution of movement following the local application of heat to some point in the course of a mature axis of *Mimosa pudica* may be reproduced in a suitably arranged piece of apparatus (Plate I, Fig. 1). This consists of a stout, upright metal tube closed at the upper extremity, provided with a number of slender, short lateral branches, and with a closely fitting stop-cock inserted at such a point in its length that some of the branches lie to its proximal and others to its distal side. The branches are open at their extremities, and can readily be connected with suitably weighted pieces of glass-tubing by flexible joints of rubber-tubing. The majority of the glass tubes are sealed at the end, but one or more of them are drawn out into fine capillary ends and left open. Their weight ought to be such as to secure a certain amount of flexion of the rubber-joints when the apparatus is filled with water. If the lower end of the main tube be connected with a stream of water under a sufficiently high pressure and the stop-cock be left open, fine jets of water will, of course, escape continuously from the capillary extremities of the open tubes, and the flexion of all the rubber-joints will diminish as pressure rises, with corresponding erection of the glass tubes connected with them. But, on sudden closure of the stop-cock, escape of water will continue to occur from the capillary orifices for some time, and with this the rubber-joints will recur to their original state of flexion in all the branches situated to the distal side of the stop-cock, whilst all those on the proximal side will retain their position of erection unaltered. Here, then, we have a distribution of movement exactly parallel to that occurring in the case of mature axes of *Mimosa* on local application of heat at some point in their course. The distal discharge of water from the capillary orifices represents transpiratory loss, the stream of water entering the lower extremity of the main tube represents root-supply, and the rubber-joints represent portions of tissue, like those present in the motor organs of the leaves, which are liable to undergo rapid alterations in strength in connection with alterations in the relations between general supply and loss of water. The sudden closure of the stop-cock suddenly obstructs all further access of water to the distal part of the apparatus, and as distal loss continues, a rapid fall in pressure takes place throughout the whole distal parts of the apparatus, the rubber joints cease to be turgescent, and the position of the glass tubes comes to be that which is determined by mere passive structural properties. But in the proximal part of the apparatus the conditions of water-supply and loss remain unaltered, or, if anything, a rise in pressure takes place, and hence there is no weakening of the joints or depression of the branches. In those cases in which centripetal movements occur in connection with the application of heat to mature axes of *Mimosa pudica*, these movements are no doubt dependent on centripetal extension of the obstructive gaseous expansion, so far as to involve the portions

of the water conducting system concerned in the supply of the leaf which moves They occur only when the point of application is immediately above the site of origin of a petiole, and they never extend beyond that leaf

Not only are the effects which are produced by so called "stimuli" in giving rise to movements in the leaves of *Mimosa pudica* profoundly modified by the presence of external conditions affecting supply and loss of water, but the effects which follow the action of individual "stimuli" differ in connection with the degree to which the latter are of a nature to give rise to disturbances in the relations of general supply and loss At any given period it will be found that simple contact disturbance gives rise to less effect than section or other interruption in the continuity of the tissues does, and that the latter, in its turn, is less efficient in giving rise to movement than the application of strong heat is

When soil and air are alike humid, contact "stimulation" occasions purely localised effects If pressure be applied to the under surface of the primary pulvinus or the upper surface of the primary petiole, full depression of the latter takes place, but the distal portions of the leaf show not the faintest traces of movement, the secondary rachises remaining fully divergent, and the pinnules in the maximal diurnal position of expansion Under similar circumstances the movements of individual pinnules which have been subjected to contact are equally purely localised, so long as displacement of one does not imply mechanical disturbance of another The movements of individual terminal pinnules are, of course, not necessarily liable to give rise to any considerable mechanical disturbance elsewhere, but, in the case of all the others, a disturbing influence is introduced by the fact that they are ordinarily set upon the rachis at such narrow intervals that, when in the diurnal position, the posterior half of each lamina overlaps the anterior half of the lamina of the pinnule situated behind it on the rachis (Plate V, Fig 3) Owing to this arrangement the sudden elevation of any pinnule must necessarily give rise to a certain amount of upward pressure on the one in front of it In spite of this, however, purely localised pinnular movements may very readily be evoked even in perfectly normal leaves when conditions of telluric and atmospheric moisture are very high Where conditions of moisture are not so excessive movements in normal leaves are liable to extend beyond the primarily affected pinnule for a certain distance along the rachis in a centrifugal direction Under these circumstances, in order to obtain perfectly localised pinnular movements, it is necessary to select particular leaves for experiment It is not at all unusual to meet with leaves which deviate so far from the normal standard as to have their pinnules set on so far apart that, when in their maximal diurnal position, they do not overlap one another, but stand quite free and apart as those of *Leucaena glauca* normally do In such leaves it is quite easy to show that, even when conditions of humidity are only moderately high, pinnular movements evoked by contact are purely localised In such cases it is easy to cause full displacement of alternate pinnules all along one or both sides of the rachis without inducing the slightest movement in the intermediate ones which are not directly subjected to contact The displacement may be caused either by pressure on the upper surface of the tertiary pulvinus or on the under surface of the lamina in both cases alike the movement remains strictly localised When atmospheric and telluric humidity

fall to a low level and temperature is high, it is very difficult to secure strictly localised pinnular movements, or even strictly localised movements in the primary petioles; action almost invariably being diffused along the course of the rachis to some extent in the case of pinnular "stimulation," and sudden depression of the primary petiole being followed by pinnular action in one or more of the secondary rachises, and in some cases by varying degrees of convergence of the latter themselves. The diffusion of movement subsequent to sudden depression of the primary petiole is no doubt mainly owing to the sudden upward pressure to which the pinnules are exposed from the air during the course of the rapid descent of the leaf, and to the fact that, in the position of full depression, leverage comes in to make for convergence of the secondary rachises. These agencies are incapable of giving rise to any appreciable effects under the conditions of relatively stable equilibrium present in connection with excessive telluric and atmospheric humidity, but are liable to produce some effect under conditions in which the drain upon the actively turgescent tissues of the motor organs is higher. In any case, contact-"stimulation" is a factor affecting processes of local filtration, but it will naturally give rise to different ultimate effects according to the degree to which the turgescent tissues are already exposed to active drain of liquid. The upward pressure of the air on the rapidly descending laminar surfaces in cases where the primary movement is one of petiolar depression, replaces the upward pressure which any primarily displaced pinnule normally exerts on its distally situated neighbour. Just as primary petiolar depression is followed by an entire absence of pinnular movements under conditions of high humidity, so in many cases under similar circumstances the elevating action of the primarily displaced pinnule is insufficient to give rise to anything save a certain amount of flexion in the lamina on which it acts, without any evidence of any alteration in pulvinar turgescence.

The mutual relations of the laminar surfaces of adjacent pinnules is amply sufficient to account for diffusion of movement as a mere result of diffusion of conditions favouring filtration, so long as the movements follow a centrifugal direction only. The successive laminæ in their mutual relations precisely correspond to the successive cards or blocks of wood in the old familiar childish game of "Jack going to market." Primary displacement of one at one end of the series is all that is necessary to secure the propagation of movement along the entire line. If the anterior cards or blocks be firmly supported,—if they be in a condition of stable equilibrium—an impulse from their posteriorly situated neighbours, which would amply suffice to give rise to displacement under conditions of unstable equilibrium, will fail to produce any appreciable effect. The propagation of movement along the series—the "irritability" of the apparatus—rises with the instability of equilibrium just as it does in the case of the pinnules. Whilst this is so in regard to centrifugal diffusion of movements along the course of the secondary rachis, centripetal propagation cannot be so simply accounted for; as there is no satisfactory evidence that, when in full diurnal position, each successive lamina exerts any considerable active downward pressure on the upper surface of the one behind it. It is possible, however, that such pressure may, in certain cases at all events, be present in some degree, and in so far as it is, its sudden removal on the elevation of the depressant pinnule must, of course, be equivalent to a rise in the relative strength of the inferior pulvinar parenchyma of the depressed pinnule, and consequently a factor calculated to give rise to disturbance in the equilibrium of position in the latter. The fact, however, that movement of

the pinnules originating in connection with contact is much less liable to be diffused to any considerable extent centripetally than centrifugally, seems to indicate that any such removal of pressure is a factor of no considerable importance, and it appears probable that the spread of centrifugal movement is aided by, and that of centripetal movement mainly dependent on, the action of an agency of a perfectly distinct nature

So long as transpiratory loss is low and root supply of water is abundant, the primary filtrative discharge of fluid incident on the local increase in pressure caused by contact implies a mere local redistribution of water and no diminution in the stock available for the maintenance of turgescence The mechanical disturbance ensures an increased activity of filtrative discharge and corresponding decrease in turgescence in certain masses of tissue, but it does not interfere otherwise with the assimilatory activity of the protoplasts on which the osmotic capacity of the cell sap and consequently the turgescent capacity of the cells depends. On the cessation of the filtrative disturbance, they will, therefore, at once begin to regain their normal state of turgescence, and, owing to the abundance of water which is available, they will readily be able to do so without in any way interfering with the turgescence of neighbouring elements But where conditions of humidity are such that turgescence is only maintained as the result of an exact equilibration between root supply and transpiratory loss, this is no longer the case A certain amount of the water discharged from the turgid elements of the active tissues, all of it, at all events, which passes into the intercellular system of spaces, is liable to be rapidly removed under the influence of continued active transpiration, and this, under the circumstances, implies an absolute diminution in the entire stock available for the up keep of turgescence The tissues which primarily lost turgescence in connection with increased filtration remain as active as ever They are just as eager to satisfy their osmotic capacities as they were before, and in their efforts to do so they must tend to interfere with the supply of neighbouring tissues just in proportion to the amount of actual loss in the general stock of water which was induced by the primary filtrative discharge The spread of movements along the course of a rachis must certainly be favoured by such a disturbance in the supply of water, and, as in normal leaves it is very difficult to secure that any mechanical disturbance has been primarily strictly localised to one or other of the individual pinnules, it is little wonder that, in the presence of external conditions implying maximal instability of position, a certain extension of movement should occur even in cases in which the direct mechanical action of the moving pinnules upon their neighbours cannot fully account for the phenomenon In any case, the movements following contact have a very limited extension and, under circumstances in which the evidence of other so called stimuli is followed by more or less extensive propagation of movement, they are normally strictly localised to the points primarily affected They do not in themselves necessarily involve any actual loss of liquid, but mere temporary redistribution of it, and hence they are not in themselves efficient causes of widely diffused disturbance in the relations of supply and loss of liquid in the actively turgescent tissues

This is no longer the case when the primary agent in determining the occurrence of movement is a rupture in the continuity of the tissues Incision of the axis or petiole, or amputation of portions of the laminæ of pinnules, is followed not merely by movements,

but by a discharge of liquid from the cut surfaces. In most cases the discharge is very conspicuous; and, under circumstances in which movements do not occur very rapidly, it can readily be determined that it is the primary result, and that movements only ensue at an appreciable interval after its occurrence has begun to manifest itself. For example, if the tip of a pinnule be gently amputated at a time when telluric and atmospheric humidity is excessive, and if all contact disturbance of the tertiary pulvinus have been successfully avoided, no movement whatever occurs for a considerable interval. But during this interval conspicuous exudation occurs on the cut surface, a prominent droplet of liquid appearing on the divided extremity of the midrib, and smaller drops presenting themselves near the margins of the lamina over the cut ends of veins. But wherever active exudation of this nature is present, we have to deal with conditions which imply no mere local redistribution of liquid throughout the tissues, but an active discharge and loss of a portion of the general stock of liquid available for the up-keep of turgescence, and hence a disturbance in the pre-existent equilibrium between supply and loss. This disturbance must necessarily be liable to extend to a greater or less degree according to the actual amount of loss which takes place and to the conditions of the tissues, of the soil, and of the air at the time at which it occurs. There is, therefore, good ground to expect that such "stimulation" should be more frequently and more extensively followed by phenomena of diffusion of movement beyond the site of primary origination than is "stimulation" by agencies giving rise to mere alterations in local pressure and filtration. Even the most casual observation is amply sufficient to show that this theoretical demand is fully met by actual fact. Whilst isolated pinnular movements are, under average conditions of humidity, the normal sequence of contact-"stimulation," purely isolated movements are quite exceptional phenomena, only occurring in association with conditions of excessive humidity, after incision of the tissues. Where conditions of atmospheric and telluric humidity are, and have for some time been, excessively high, amputation of the tip of a lamina is occasionally followed by movement in the injured pinnule only, or, in the case of heavily-laden leaves, by action in it and the primary pulvinus alone; but, under conditions of average humidity, and at times when contact is followed by strictly localised movement in the primarily affected pinnule, amputation or incision of the tip of a pinnule is followed by movements extending along the entire course of that secondary rachis, at least. Where conditions of humidity are higher, the propagation of movement becomes more limited and extends only partially over the course of the rachises; and, on the other hand, when conditions are such that contact is liable to be followed by diffusion of movement, incision or amputation is attended by movements which are often propagated throughout the entire area of the leaf. When contact-"stimulation" is attended by strictly localised movement, incision or amputation is ordinarily followed by movements extending over a portion of the leaf, and when contact is attended by a limited amount of diffusion of movement, incision or amputation is ordinarily followed by movements extending throughout the entire leaf. The only possible explanations of these differences are either that incision is a stronger stimulant to protoplasmic contraction, or a more efficient determinant of alterations in the pre-existant relations between supply and loss of liquid than contact is. According to the ordinarily accepted theory we must assume that it is the former without, however, having any independent evidence that it actually is so; according to the purely physical theory of movement we are not obliged to make any groundless assumption, as the phenomena are such as to leave no room for doubt that it actually does give rise to greater

disturbance in the relations between loss and supply of liquid than any mere contact is capable of determining.

There can be no question that rupture of the continuity of the tissues by incision is a much stronger determinant of the diffusion of movement than mere contact impulses are, but in this respect it falls far short of injuries effected by means of heat. The movements attending the application of an open flame, of highly heated metal, or of the carefully focussed rays of the sun to individual pinnules are never of a strictly localised nature Even under conditions of maximal humidity a certain amount of diffusion of movement occurs, under circumstances when incision is followed by movements extending over the entire secondary rachis to which the primarily injured pinnule belongs, the application of heat gives rise to movements extending over the entire leaf, and when incision is followed by movements extending over the entire leaf, heating is followed not merely by these, but by movements in a varying but sometimes considerable number of leaves along the course of the axis to which the primarily affected one is attached This may at first sight appear as though it were adverse to the physical theory of movement, and only explicable as the result of the presence of differences in degree of specific protoplasmic stimulation, but it is only to casual observation that it does so. The evidence of the occurrence of any considerable exudative loss of liquid from the tissues is certainly not as a rule so conspicuous as it is, in cases where the continuity of the tissues is interrupted by means of incision. This is, however, in great part explicable as the result of the different conditions to which any exudation is exposed in the two cases In cases of incision we are dealing with mere rupture in the continuity of the tissues, and, so long as atmospheric humidity is not excessively low, any liquid which escapes naturally tends to accumulate locally, and therefore to appear conspicuously But where the tissues are injured by the application of heat, localised conditions for excessive evaporation are necessarily present, and therefore an absence of local accumulation of liquid does not imply an absence of local exudation. Where a considerable mass of soft succulent tissue is present, as in the case of young axes, the local application of heat is often followed by conspicuous indications of exudation even in spite of the attendant excessive evaporation, but when the mass of tissue is limited in relation to the heat, as it is in the case of pinnules, the rapid evaporation masks the discharge. The rise in evaporation, moreover, is not of course strictly localised to the spot to which the healing agent is directly applied, but must extend over a certain area beyond this, so that there is not mere local exudation and evaporation from the actually injured tissues, but a cause for sudden increase in transpiratory loss in neighbouring and intact ones This in itself is sufficient to account for the fact that heat should be a more efficient determinant of movement than incision is In cases of incision the primary alteration in the condition of the tissues is a strictly localised one, whilst, in cases where heat is applied, there is not merely intrinsic local change in the tissues in the immediate site of application, but an alteration in the extrinsic conditions to which neighbouring tissues are exposed. But another circumstance also comes in to render heating a more efficient cause of extensive movement than simple rupture of the continuity of the tissues is The liquid which exudes from the tissues on incision very rapidly evaporates and condenses when exposed to the air, and soon forms a protective stratum precluding farther escape from the divided surfaces, and as the local injury to tissue is extremely limited, the site of incision ceases to be a weak

point in respect to relations between supply and loss of water. The abnormal drain on the general stock of liquid within the tissues is purely temporary in cases of incision. But this is no longer the case where portions of tissue are killed by application of heat. Any ordinary application of heat to a particular point implies the death of considerable masses of tissue and, as we have already seen, any dead mass of tissue represents a permanent site of abnormally excessive drain upon the general stock of liquid. The details which were given in Chapter II regarding the phenomena occurring in connection with the death of portions of axes or rachises under the influence of the vapour of chloroform and heat are sufficient to show that this is the case; and the fact is of course constantly brought before us by the difficulty which is encountered in keeping portions of a leaf or shoot turgid beyond any point in which the tissues have been killed by means which do not in any way interfere with the efficiency of the water-conducting system, whenever external conditions are such as to favour active evaporative loss. In cases of the application of heat, then, we do not merely determine temporary exudative and evaporative loss in the site of application and its immediate neighbourhood; but we also almost inevitably establish a permanent abnormal drain upon the water-supply generally, and with this the liability to diffusion of movements naturally increases.

In cases of contact-"stimulation" we induce mere local redistributions of liquid within the tissues; in cases of incision we give rise to temporary exudative loss from the general supply of liquid; in cases of heating we secure not only this, but in addition we establish temporary increase in transpiratory loss and a site of persistent abnormal drain. The tendency to diffusion of movement is at a minimum in cases of contact; in cases of incision it increases; in cases of heating it rises to a maximum. The two sets of facts run parallel with one another, and the former of them affords an explanation of the latter, if we accept the view that the movements are dependent on fluctuations in the relations existing between supply and loss of liquid. If, on the other hand, we insist on adhering to the popular theory, we must be content to assume that contact, incision, and heat are stimuli which differ from one another in their capacity for inducing active protoplasmic contraction.

CHAPTER XII.

The causes of the propagation of movements in Mimosa pudica.

Whilst the movements of the various parts of the leaves of *Mimosa pudica* have by common consent been ascribed to the action of certain special masses of irritable and contractile tissue in the motor organs, several distinct theories have been advanced to explain the phenomenon of the diffusion of movements beyond the site in which they are originally induced, or, according to the ordinarily accepted theory, to explain the diffusion of "stimulation" from one part to another. According to the older observers, Dutrochet, Sachs, Hoffmeister and Pfeffer, fluctuations in the pressure of the current of liquid traversing the wood played the part of mechanical stimuli to the irritable and contractile elements in the tissue of the motor organs. At a later period, and when attention was first attracted to the fact that, as a general rule, the protoplasts of vegetable tissues are not isolated, but are connected with one another so as to form a continuous reticulum, an attempt was made to substitute a nervous for a mechanical theory

of propagation Finally, Haberlandt has reverted to the older view with the modification that, according to him, the stimulant fluctuations in liquid pressure do not normally traverse the wood, but the system of large sieve tubes in the soft bast which he regards as constituting a specific "*Reizleitende system*" His theory agrees with that of the older writers in regarding fluctuations in liquid pressure as serving as mechanical stimuli to the specific contractile apparatus in the motor organs, but affirms that such stimulant fluctuations are practically solely diffused by means of the sieve tubes of the soft bast He does not question the existence of special irritable and contractile tissues in the motor organs, but merely modifies the older view in regard to the precise paths followed by the agencies which are assumed to call these into activity His theory is mainly founded on the fact that he was able to demonstrate that the liquid which exudes from the tissues when they are incised is not mere water, as it should be if derived solely from the wood, but is in great part composed of materials which are evidently derived from the sieve tubes of the bast No one can deny that he has successfully demonstrated this, and has added greatly to our knowledge of the histological details of *Mimosa pudica*, but he has certainly not succeeded in proving that his "*Reizleitende system*" is specifically and essentially related to the phenomena of propagation of movement. His own experimental results indeed force him to allow that propagation may occur in spite of the entire absence of his conducting system throughout considerable areas of tissue, but notwithstanding this, his desire to establish the presence of a specific mechanical nervous apparatus leads him to adhere to his theory When he found that propagation extended beyond areas which had been entirely denuded of his "*Reizleitende system*," and is forced to allow that in such cases diffusion of impulses must have taken place through the wood, it might have been expected that his views as to the specific value of the system of sieve-tubes would have undergone some modification, but apparently they were too firmly subjectively established at the time at which he made the observation to be shaken by any facts which conflicted with them He had, of course (although he does not appear to recognise it) equally clearly demonstrated the fact that propagation could occur apart from the presence of any continuous system of turgid sieve tubes, in the experiments on which he founds his decisive rejection of the theory of propagation by means of continuity of living protoplasts In these experiments he killed the tissues of a certain area in the course of the petioles of leaves by means of boiling them, and then determined the fact that "stimulation" applied at one side of the dead area was followed by the occurrence of movements on the other side Now this, no doubt, very satisfactorily demonstrated that diffusion of movement could not be essentially dependent on the propagation of impulses along continuous tracts of living protoplasm, but it just as effectually proved that it was not necessarily owing to any propagation of impulses along the course of continuous system of turgid sieve tubes The boiling of the petiolar tissue secured the interposition of an area of dead protoplasm, but it just as certainly secured the interposition of an area devoid of turgidity, and in addition to this of an area within which an abnormal leakage of water was present He was evidently aware of the latter fact, as he specially alludes to the necessity which arises in such cases of taking special means to prevent the drying up of the parts beyond the boiled area, but, in spite of this, he appears to assume that the turgidity of the sieve tubes remained intact The position is an incomprehensible one, he demonstrates that the presence of a continuous system of turgid sieve-tubes, and even

that the presence of sieve-tubes at all, is unnecessary for the occurrence of propagation of movement, and yet maintains that the presence of such a system is specifically related to the phenomenon.

The results which may be obtained where areas in the course of entire axes in place of petioles are killed by means of the local application of heat are even more convincing. Areas of a quarter of an inch in length in the course of axes may be readily killed by boiling, or more conveniently by thoroughly searing them with heated forceps. It is easy to kill several successive areas at intervals along the course of a single axis, and yet propagation of movement will take place from points on the proximal side of the lowest dead area to points situated on the distal side of the highest one. For example, taking a small plant and searing the axis in two points so that one or more leaves are situated below the lowest seared area, one leaf between the two seared areas, and several beyond the distal seared area, it will be found that, when external conditions are such as to favour the occurrence of propagation of movements, the application of heat to the base of the axis is followed by action in all the leaves alike, whether beneath, between, or beyond the seared areas (*vide* Appendix G). It is easy to determine in such cases, by means of sections carried through the entire thickness of the axis, that the tissues have been completely killed throughout (Plate V, Fig 7). This, of course, demonstrates that any continuity of living protoplasm is unnecessary, and on Haberlandt's theory forces us to assume that the initial impulses originating in his specific conducting system undergo a primary transfer to the wood, a return to the specific conducting system, a renewed transfer to the wood, and a renewed transfer to the specific conducting system, ere they tell on any leaves situated beyond the distal seared area. Surely the specificity of the "*Reizleitende system*" is, under such circumstances, hard to recognise.

But it is not only by such experiments that the groundlessness of Haberlandt's assumption may be demonstrated. The phenomena, which have been already described as following the local application of heat to points in mature, hard axes are equally conclusively opposed to it. In such cases, if the diffusion of movement were essentially dependent on the propagation of fluctuations in pressure along a system of tubes filled with liquid, it ought assuredly to take place in both directions alike. But this it most certainly does not do; for, whilst granting that external conditions are favourable to the occurrence of movements, centrifugal diffusion normally occurs with the greatest certainty and to an indefinite extent, centripetal diffusion is normally entirely absent, and, in the exceptional cases in which it does occur, is entirely limited to the very immediate neighbourhood of the site at which heat is applied. In any continuous system of tubes filled with liquid, the local application of heat to any particular point in its course must inevitably give rise to an increase in pressure which must be propagated in both directions alike; and, if increase in pressure throughout the system were an essential factor in determining the occurrence of movements, movements would certainly manifest themselves in both directions, alike. But as a matter of fact, the rise in pressure is propagated in both directions, whilst movements occur only in one.

Haberlandt is unquestionably right in maintaining that much of the liquid which exudes from the tissues of *Mimosa pudica* on incision is derived from the highly turgid tissues of the soft bast, but the latter do not hold any truly specific relation to the occurrence of propagation of movement. They provide an apparatus facilitating the sudden escape of liquid from the tissues, and hence an apparatus facilitating sudden

fluctuations in the liquid contents of the latter, but here their relation to the occurrence of propagation of movements ceases. Their excessive turgidity and their structure render them effective agents in securing the loss of large quantities of liquid on incision, and this provides for a disturbance in the pre-existent equilibrium between supply and loss of liquid generally. Their excessive turgidity secures a large discharge of liquid and their high osmotic capacity, on which their normal turgescence depends, must render them a source of excessive drain upon the generally available stock of liquid. Any sudden discharge of a large quantity of liquid from them implies a suddenly increased demand upon the general water supply, and, owing to their excessive osmotic capacity, they are well adapted to worst other active tissues in the struggle which must ensue until a condition of liquid equilibrium be once more established. As has been already pointed out, the presence of any extensive system of excessively osmotic elements is in itself an element favouring instability of equilibrium on the relations between general loss and supply of liquid in less highly osmotic tissues. When any great loss in turgidity occurs within it, apart from any alteration in its functional activities, and consequently of its osmotic capacity, the latter co-operates with active transpiratory loss in giving rise to a great draught upon the general stock of fluid available for the maintenance of turgescence, whilst the coincident fall of pressure probably induces additional filtrative escape from other active tissues. The "*Reizleitende system*" is an apparatus through means of which the conditions of equilibrium between general supply and loss of liquid may be very readily disturbed and, therefore, is an apparatus through means of which movements may readily be indirectly determined, but is not peculiar or specific in this respect for, as we have already seen, similar effects may be produced by means of changes taking place within the wood.

Haberlandt affirms that any fluctuations of pressure within the system of seive tubes, whether of a positive or negative nature, are capable of acting as stimulants to the contractile tissue of the motor organs. But the phenomena attending the local application of heat to mature, hard axes show that fluctuations of pressure within it are not necessarily efficient factors in determining movements, and also that it is only negative fluctuations in general liquid pressure that are anywhere efficient. In such cases we have positive fluctuations in liquid pressure arising within the sieve tubes in both directions alike, and movements occurring only centrifugally, that is in the direction of diminished liquid pressure, within the water conducting system. Negative fluctuations in liquid pressure in these cases occur in all distally situated areas in consequence of the obstructive expansion of the gases of the water conducting system, in cases of incision, on the other hand, similar fluctuations arise both centripetally and centrifugally owing to the sudden escape of considerable masses of liquid from the tissues. In the first instance, movements occur only centrifugally, in the second both centripetally and centrifugally, in other words, in both instances alike, the distribution of movements coincides with the distribution of negative fluctuations in liquid pressure. Such fluctuations may arise in various ways, they may arise in consequence of escape of liquid from the system of sieve-tubes, of obstructions arising in the water conducting system of the wood, of sudden contraction in the gaseous contents of the latter, of increased transpiratory loss, or of sudden arrest of root supply connected with separation from the axis, and in all cases alike they are liable to be followed by the occurrence of spreading movements. Negative fluctuations in general liquid pressure are the specific determinants of all spreading movements which

are not mechanically produced by the relation of neighbouring parts, as in the case of adjoining pinnules; but there is no one specific apparatus by which such fluctuations are determined.

Movements may be induced by the action of three distinct factors: by fluctuations in the osmotic capacity of the tissues of the motor organs, by fluctuations in the conditions affecting processes of local filtration within the motor organs, and finally, by fluctuations in the conditions of general supply and loss of water. The normal periodic nyctitropic movements of the leaves, or those arising under the influence of exposure to anæsthetics, are determined by the action of the first of these factors; the movements following contact are primarily determined by the second; those following incision or heating of the axis, or those attending excessive transpiration by the third. We have thus to deal with three distinct classes of movements in so far as their causation is concerned, and it is only in connection with one of these that phenomena of propagation manifest themselves. The effects of anæsthetics or of partial deprivation of light are strictly localised to the areas directly subjected to the abnormal conditions, and within which depression of functional activity, and consequently of osmotic property, takes place. Movements induced by local increase in filtration, where this alone comes into play, are equally unattended by any diffusion. It is only where, and only so far as, conditions affecting the relations of general supply and loss of water are present that any propagation of movement occurs; and, finally, it is only when and so far as such conditions effect negative fluctuations in the supply of water available for the maintenance of turgescence, that they are efficient in giving rise to propagation of movements.

E. J. H.—Reg. No. 6466J—320—18-12 94.

APPENDIX A

THE EFFECTS OF DISTAL LEVERAGE ON THE POSITION OF THE PRIMARY PETIOLE OF THE LEAVES OF *MIMOSA PUDICA*

When detached shoots of *Mimosa pudica* are set in water and have a fresh absorptive surface provided by subaqueous amputation of their lower ends, the pinnules under the influence of light presently assume their normal diurnal position, unless atmospheric humidity be abnormally low, or when they are exposed to the influence of direct sunshine The primary petioles, however, ordinarily remain somewhat depressed If now all the pinnules be gently cut off no sensible increase in petiolar depression usually occurs in spite of the escape of a certain amount of liquid from the tissues which necessarily attends the procedure, and presently steady progressive elevation of the petioles sets in The amount of absorption of water taking place at the cut extremity of the shoot is insufficient to secure elevation of the petioles so long as the inferior parenchyma of the primary pulvinus has to contend with the normal leverage of the distal portions of the leaf, but suffices to do so when the leverage is considerably reduced by the removal of the pinnules

Extreme elevation of the primary petioles occurs under the following conditions —I Prolonged depression of assimilatory function with continued respiratory loss and suppression of transpiration, such as takes place during the course of the night II Exposure to an environment implying excessive transpiratory loss III Amputation of the pinnules or pinnæ The only common feature which these conditions present is that they all imply the establishment of a considerable reduction in distal leverage

Sudden, rapid movements of elevation of the primary petioles corresponding to the common sudden movements of depression, which so constantly manifest themselves, are of very rare occurrence This is owing in part to the inherent structural features which distinguish the inferior and superior masses of parenchyma in the primary pulvinus and partly to the fact that the superior mass is co-operated with by distal leverage, whilst the inferior one is directly opposed by it Visibly progressive movements of elevation, and even sudden, rapid movements of a similar nature do, however, manifest themselves under certain circumstances When a plant is enclosed within a saturated atmosphere and exposed to diffused sunlight, extreme expansion of the distal portions of the leaf and maximal elevation of the primary petioles occurs If now it be suddenly exposed to relatively dry air, and consequently to sudden transpiratory loss, elevation of the pinnules and deep depression of the primary petioles occurs almost immediately in the majority of the leaves, and on returning it to the saturated atmosphere petiolar elevation sets in at once and progresses so rapidly as to be readily visible to the unaided eye In such cases the movements of elevation, although rapid, are not of a sudden character, but movements of elevation, as sudden as any common movements of depression are, may be induced by exposing the pulvinar tissues to circumstances inducing sudden losses in turgescence primarily localised to the superior parenchyma If the rays of the sun be carefully focussed upon the upper surfaces of primary pulvini, the first movements which manifest themselves are in many cases sudden movements of elevation of the primary petiole The following table shows the results of fifteen experiments of this nature which were conducted on two successive mornings, and it will be seen that in nine instances sudden movements of elevation of the primary petiole occurred —

Table I —*Results of focussing the rays of the sun on the upper surfaces of the primary pulvini of leaves of* Mimosa pudica.

1 Depression of the primary petiole
2 Extreme elevation of the primary petiole, followed by depression
3 Depression of the primary petiole
4 Rotation of the primary petiole, followed by depression
5 Depression of the primary petiole

6. Strong elevation, followed by depression.
7. Ditto, ditto.
8. Ditto, ditto.
9. Depression.
10. Ditto.
11. Strong elevation, action in the pinnules; nothing more.
12. Depression.
13. Strong elevation, followed by depression.
14. Elevation; a pause; action in the pinnules; nothing more.
15. Ditto; depression.

The movements of elevation of the primary petiole occurring in such cases are, as a rule, followed by depression, because it is only initially that the loss in turgescence following the insolation is confined to the superior mass of pulvinar parenchyma, and because, when it has once extended so as to affect the inferior mass, the persistent excess in structural strength of its opponent and the leverage of the distal parts of the leaf come into play as they ordinarily do. Under circumstances implying general loss in turgescence the movements of the primary petiole are always movements of depression, because the structural features of the inferior mass of pulvinar parenchyma are such as to render it more liable to rapid losses in turgescence, and because it has constantly to struggle against, in place of being aided by, distal leverage in giving rise to the displacement which it makes for. That sudden movements of elevation should occur at all is, however, sufficient to show how unfounded is Sachs' statement that "die Unterseite allein ist also reizbar, das Parenchym der Oberseite ist nur Hilfsorgan bei der Bewegung."* There is absolutely no evidence to show that the protoplasts of the superior parenchyma are less contractile than those of the inferior parenchyma. The two masses of tissue differ from one another both structurally and functionally, but the functional differences are connected not with contractile, but with assimilatory property. The superior parenchyma is distinguished by excess in structural strength and the inferior one by excess in assimilatory activity, and it is the presence of these differences, combined with the fact that distal leverage co-operates with the superior and directly opposes the inferior parenchyma in effecting the displacements which they make for, that determines the ordinary character of the movements of the primary petiole. It is the presence of these differences and the action of distal leverage, and not the presence of any specially contractile protoplasts in the inferior parenchyma, that accounts for the fact that sudden movements of depression of the primary petiole are so common, and sudden movements of elevation quite exceptional.

The following experimental data illustrate the effect of variations in conditions of distal leverage in modifying the character of the effects following amputation of distal portions of leaves attached to growing plants:—

EXPERIMENT I.—*June 14th, 3 P.M. Rain falling heavily; pinnules as a rule elevated or partly elevated owing to recurrent agitation by rain-drops; primary petioles fairly well elevated in almost all cases.*—Amputation of the tips of terminal pinnules in leaves in which they were only partially elevated was, in all cases save two, immediately succeeded by deep depression of the primary petiole. Of the two exceptional leaves one was supported by a neighbouring one, and the other was free of any adherent drops of rain. The action in the pinnules was in all cases very slow and confined to the injured pinna, and in most cases was very imperfectly carried out. At 6 P.M. the leaves were all in full nocturnal position; but although the evening was absolutely still and excessively humid, maximal depression of the primary petioles in almost all cases succeeded the slightest contact impulses. The influence of distal leverage in assisting to determine petiolar depression comes out very clearly in regard to both periods of experiment. In the former one atmospheric and telluric conditions were such as to be manifestly unfavourable to the occurrence of rapid losses in turgescence, as the behaviour of the pinnules very clearly shows; and yet petiolar movements of great magnitude occurred with excessive frequency because of the abnormal excess in distal leverage provided by the adherent drops of rain. In the second period also, facilities for transpiratory loss were minimal, and root-supply was

* Vorlesung, XXXVII, s. 792.

excessive, and yet the primary pulvini were excessively irritable owing to absence of solar stimulation and persistent excess in distal leverage from adherent water

EXPERIMENT II.—*July 24th 3 30 P M Bright but clouded soil very moist no rain during the three previous days leaves all in maximal diurnal position with their primary petioles horizontal, slightly depressed, or very slightly elevated*—Amputation of the tip of a single pinna, or even of a single distal pinnule, was succeeded by movements extending throughout the entire leaf and including extreme depression of the primary petiole, whilst amputation of the entire distal portion of the leaf beneath the point of origin of the lower pair of pinnæ gave rise to little, and, in some cases, to no petiolar depression, and was presently followed by extreme petiolar elevation, although it was attended by conspicuous exudation on the cut surface Here there was manifestly no direct relation between the severity of the initial injury and the occurrence of petiolar movement, but very clearly a direct relation between the latter and the amount of distal leverage Had depression of the primary petiole been dependent on active contraction of the protoplasts of the primary pulvinus incident on stimulation connected with the sudden propagation of stimulant fluctuations in pressure along the course of Haberlandt's "Reizleitende system," or originating in any other fashion, this could not have been the case, as maximal fluctuations in pressure and maximal injury would under such circumstances have inevitably led to maximal in place of minimal movement But, as it is a purely physical process, the tendency to petiolar depression originating in connection with the fall in turgescence in the pulvinar parenchyma incident on the escape of liquid from the cut surfaces, although greater in cases where the entire distal parts of the leaf were amputated than where only the tips of pinnæ or pinnules were detached, was more or less discounted by the great coincident decrease in distal leverage, whilst the much smaller escape attending amputation of the tips of individual pinnæ or pinnules, not being accompanied by any appreciable diminution in distal leverage sufficed to induce extreme petiolar depression At 6 30 P M the leaves were in fully developed nocturnal position The petioles which had been deprived of pinnæ were now not nearly so highly elevated as they were shortly subsequent to the operation, but were still more elevated than those of entire leaves, the phenomena, on the one hand, indicating the effects of the loss in turgescence in the pulvinar tissues incident on the cessation of solar stimulation, and on the other the minor degree of petiolar depression attending this when distal leverage is greatly reduced in amount

APPENDIX B

THE RATE OF TRANSPIRATION IN *MIMOSA PUDICA* AND THE EFFECTS FOLLOWING DISTURBANCES IN THE RELATION BETWEEN TRANSPIRATORY LOSS AND ROOT SUPPLY OF WATER

THE rapidity of transpiratory loss is so great that the pinnules of leaves on detached axes set in water, and with their bases subsequently divided to provide a fresh absorptive surface, only very imperfectly assume the diurnal position under the influence of light unless the degree of atmospheric humidity be relatively high The activity of transpiratory loss is also very clearly indicated by the results which attend very inconsiderable diminutions in the amount of root supply as is demonstrated by the results of the following experiments —

EXPERIMENT I —A pot plant, the leaves of which were in maximal diurnal position, and which had to some extent rooted into the ground through the opening in the bottom of the pot, was carefully taken up without injury to the projecting roots and was then conveyed to the laboratory On arrival there the pinnules of all the leaves were in maximal nocturnal position, owing partly to the agitation which the leaves had been subjected to during transfer The pot was now placed over a vessel of water so that the projecting roots were immersed, and the entire apparatus was set in a sealed chamber The pinnules rapidly assumed the maximal diurnal position The pot was now removed gently from the water vessel and chamber and set on a table in the open laboratory and the pinnules once more gradually passed into the nocturnal position When they had fully done so, the pot was anew placed over the water vessel within the chamber, and within the course of twenty minutes the pinnules were once more in maximal diurnal position On a second removal from the

chamber the nocturnal position was again resumed, and was once more replaced by the diurnal one on return to the chamber. The phenomena present in this experiment not only demonstrate the extreme rapidity of transpiratory loss and the accuracy of the balance which must be maintained between transpiratory loss and root-supply of water in order to the retention of a given position by the pinnules, but also that the nocturnal position is one which coincides with minor degrees of turgescence in the motor organs, and not with increased turgescence as affirmed by Pfeffer.

The results of six experiments with regard to the actual amount of transpiratory loss taking place under favourable circumstances were as follows:—

Experiment II.—A plant with seven leaves and 222 pinnules yielded 2·31 C.C. of water in twenty-four hours.

Experiment III.—A plant with nine leaves and 579 pinnules and weighing 4·32 grammes yielded 3·40 C.C. water in twenty-five hours.

Experiment IV.—A plant weighing 4·34 grammes yielded 6·40 C.C. water in forty-eight hours.

Experiment V.—A plant weighing 2·03 grammes yielded 4·1 C.C. water in twenty-four hours.

Experiment VI.—A plant with five leaves and 194 pinnules and weighing 2·32 grammes yielded 1·5 C.C. water in four hours.

The following experiment illustrates the results following a disturbance of the normal balance between transpiratory loss and root-supply of water:—

Experiment VII.—The protruding portions of the roots of several pot-plants which had rooted into the ground were cut off. In some of the plants the branches were cut short, so as to leave only a limited number of leaves; in others they were left intact. Thirty-six hours later all the leaves on the plants with shortened branches were in full diurnal position, whilst in the plants with intact branches the pinnules were in a position intermediate between the diurnal and the nocturnal one. The only thing to account for the difference in the position of the pinnules in the two sets of plants is that in the case of those with shortened branches the transpiratory surfaces had been reduced coincidently with the absorptive ones, whereas in those with intact branches the apparatus for absorption had been diminished, whilst that determining loss of water remained as before.

The next experiment also illustrates the effects attending disturbance of the equilibrium between supply and loss of water, only in it the absorptive surface was an abnormal one, consisting of the divided extremity of the axis in place of being radicular.

Experiment VIII.—A detached shoot was fixed upright, so that its lower extremity dipped into a vessel of water and was exposed to diffused sunlight. At 11-23 a.m. the pinnules were all almost in full diurnal position. The water-vessel was now carefully removed without in any way disturbing the shoot, and at 12-7 noon the pinnules were all more or less highly elevated. The water-vessel was now replaced and a fresh absorptive surface provided by subaqueous division of the lower end of the axis, and at 2-20 p.m. the pinnules had almost all regained the normal diurnal position.

The results in experiments like the two preceding ones are precisely parallel to those attending exposure to hot and dry air, but are induced, not by increased loss, but by diminished supply of water. In order to establish a tendency towards the assumption of the nocturnal position all that is necessary is that the pre-existent equilibrium between supply and loss of water should be disturbed in such a fashion as to cause the latter to undergo a relative increase. Such relative increase may arise either as the result of diminished supply or of increased loss, but in any case the effects which it produces are the same. In the case of normally rooted plants an excess of loss may arise in consequence of excessive aridity and temperature of the atmosphere such as frequently prevails at midday and during the course of the afternoon, and hence under such circumstances a spontaneous assumption of the nocturnal position frequently manifests itself in spite of the fullest solar stimulation of assimilatory activity. In the case of plants with partially exposed roots, or of detached shoots, a similar diurnal assumption of the nocturnal position attends any sudden arrest or considerable diminution in supply of water even when conditions are unfavourable to the occurrence of excessive transpiratory loss. In the former case recovery of the normal diurnal position attends a diminution in transpiratory loss; in the latter it follows the renewal of water-supply, conditions of transpiratory loss remaining unaltered. It is relative diminution in loss in either case which determines the resumption of the normal diurnal

position, and such diminution may be effected as the result either of absolute diminution in loss or of absolute increase in supply Hence normally rooted plants which have passed into the nocturnal condition diurnally may be caused to resume the normal diurnal one by exposing them to conditions implying either diminished transpiration or increased root supply in other words, by exposing them to a more humid atmosphere, or by adding water to the soil in which they are rooted

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APPENDIX C.

THE INFLUENCE OF VARIATIONS IN DEGREE OF ASSIMILATORY ACTIVITY ON THE OCCURRENCE AND CHARACTER OF THE MOVEMENTS OF THE LEAVES OF *MIMOSA PUDICA*

VARIATIONS in osmotic capacity in the tissues of the motor organs connected with variations in the activity of assimilatory function come into play as intrinsic factors affecting the liability of the leaves to undergo sudden movements. The degree of "irritability" of plants exposed to conditions implying excessive atmospheric and telluric humidity is conspicuously much greater after sundown than whilst they are exposed to full solar stimulation, and, whilst the sudden exposure of a plant to the arid atmosphere of a simple sulphuric acid chamber is only attended by slow and gradually progressive movements of the leaves, exposure in a chamber containing both sulphuric acid and chloroform is followed by the occurrence of rapid pinnular movements Osmotic capacity in the cell sap determines the existence of turgescence, and in maintaining it has constantly to contend with the filtrative escape of liquid incident on the elastic recoil of the extended cell walls Any fall in osmotic property in the cell sap must favour the occurrence and rapidity of processes of filtration, and consequently the occurrence of rapid fluctuations in the degree of turgescence of the tissue, hence factors, which are quite incapable of giving rise to rapid and considerable fluctuations in turgescence whilst osmotic capacity is high, may well become efficient to do so when it has undergone considerable decrease The effect produced by any factor favouring the escape of liquid from the interior of the cell cavities, and consequently making for diminution in turgescence of tissue, must necessarily be modified by the degree of osmotic capacity in the cell sap which is a factor making for local retention of liquid Consequently depression of assimilatory activity, as it normally implies a decrease in osmotic capacity, not only comes into play to give rise to slow, progressive movements when it acts alone, but has also an important influence in modifying the extent to which the sudden incidence of other factors making for decreased turgescence will be capable of giving rise to the occurrence of sudden movements The ordinary periodic movements of the leaves are manifestly determined by fluctuations in turgescence in the tissues of the motor organs connected with fluctuations in the degree of assimilatory activity incident on the presence or absence of solar stimulation, and it is evident that any other factors of fluctuations in turgescence must be liable to have their effects modified according as they act in unison with, or in opposition to, the assimilatory influences affecting turgescence The removal of solar stimulation determines the occurrence of a fall in turgescence which makes for the assumption of the nocturnal position, and if another factor making for the same thing comes into play simultaneously with it, it is evident that the effect which the latter will produce is likely to be greater than when it comes into play at a time when the conditions of assimilatory activity, in place of favouring the assumption of the nocturnal position, favour the maintenance of the diurnal one Hence, other things being alike, "irritability" tends to attain its maximum at sundown owing to the fact that, at this time, any factor making for decreased turgescence acts in co operation with a coincident fall in assimilatory activity which makes for the same thing The absence of solar stimulation, however, not merely favours the occurrence of rapid movements under the influence of other factors making for losses in turgescence in the motor organs, but also affects the permanence of the position which has been assumed under the influence of the latter. That this is the case is clearly demonstrated by the results of experiments such as the following one —

EXPERIMENT I —A shoot of *Mimosa pudica*, bearing five leaves, was detached from a plant at 6 40 A M without any special precaution to avoid disturbance of the leaves all of which, as is usual under

normal circumstances, acted fully as regards their primary petioles and pinnules, but showed hardly any appreciable pinnal convergence. It was at once placed in a dark, moist chamber, which was allowed to remain closed until 8-20. When the chamber was opened, the position of the various parts of the leaves was found to be just the same as it was when they were enclosed in it. The shoot was now removed from the chamber, laid on a table in front of a window and covered by a bell-glass. Within a short period the primary petioles gradually became partially elevated, and the pinnules assumed the normal diurnal position almost completely. Two hours later the petioles remained as before, but the pinnules had assumed a position intermediate between the normal diurnal and nocturnal ones. According to the ordinarily accepted theory of the causation of the movements in the leaves of *Mimosa pudica*, we are called on in this instance to believe that the primary depression of the petioles and elevation of the pinnules were dependent on stimulation and active contraction of the protoplasts of the motor organs of the primary and tertiary pulvini incident on a factor—separation from the axis—which failed to act as an appreciable stimulant to the protoplasts of the secondary pulvini; that this condition of stimulation and active contraction lasted continuously for nearly two hours whilst the shoot remained in the dark and deprived of any solar stimulus; that it was then replaced by a condition of relaxation on exposure to the influence of light; and, finally, that continued exposure to light acted as a stimulant to the contractile protoplasts of the tertiary pulvini, but failed to do so to those of the primary ones. It is surely more rational to explain the sequence of phenomena in the following fashion. The primary depression of the petioles and elevation of the pinnules were dependent on the sudden disturbance of liquid equilibrium throughout the tissues, caused by the sudden arrest of root-supply of water and the active escape of liquid accompanying separation from the axis. This depressive disturbance was sufficient to give rise to considerable filtrative discharge of liquid, and consequent loss in turgescence, in those sites in which *special structural facilities* for the escape of liquid from the interior of cell-cavities are present, and hence movements occurred connected with sudden fall in turgescence in the inferior parenchyma of the primary pulvini and in the superior parenchyma of the tertiary ones, whilst no appreciable movements occurred in the pinnæ because of the minor facilities for rapid redistribution of liquid provided by the tissues of the secondary pulvini. During the period in which the shoot was retained in the moist but dark chamber, recovery of the diurnal position did not occur, not because there was not a stock of reserve water within the water-conducting system, or on account of active transpiratory loss, which was precluded by the atmospheric humidity of the chamber, but because the total absence of solar stimulation prevented the protoplasts of the tissues from giving origin to the unstable assimilatory products on which the osmotic capacity of the cell-sap, which is necessary to induce full turgescence of the tissue elements, was absent. On subsequent exposure to sunlight, even under conditions implying *no fresh supply* of liquid and permitting of relatively free transpiratory loss, the rise in osmotic capacity in the cell-sap was sufficient to determine active absorption of the reserve water in the water-conducting system, and therefore to determine a rise in the turgescence of the pulvinar tissues leading to a resumption of the diurnal position of the primary petioles and the pinnules so long as enough reserve water remained within the water-conducting system to more than counterbalance the coincident transpiratory loss. Finally, when (as the result of continued transpiratory loss and assimilative decomposition of water) the stock of reserve water became insufficient for this, a tendency towards the resumption of the nocturnal position set in and manifested itself earlier and more conspicuously in the pinnules than in the primary petioles, because the action of local loss of turgescence in the tissues of the primary pulvini was more or less discounted by the coincident diminution in distal leverage attending diminished turgescence in the laminar portions of the leaves.

The effects of a normal depression of assimilatory activity, or in other words of a normal decrease in the osmotic capacity of the pulvinar tissues in giving rise to a greater liability to the occurrence of movements, or as it would be commonly described to "increased irritability," is very strikingly demonstrated in connection with experiments, like the following, in which the tips of axes are gently amputated without any mechanical disturbance of the plants :—

EXPERIMENT II.—*June 3rd. Both soil and air very humid.*—At 8 A.M. the leaves were in full diurnal position. Amputation of the tips of axes was followed merely by the exudation of a great drop of liquid from the cut surface. At 7 P.M. the leaves were in full nocturnal position. Amputation of

the tips of axes was followed by no conspicuous exudation, but by centripetal propagation of movements of petiolar depression to many leaves along the course of the injured axis.

EXPERIMENT III.—*August 20th. There had been heavy showers in the morning, so that the soil was saturated, but subsequently continuous radiant sunshine had prevailed* 1 P M —The plants were not exposed to direct sunshine and the leaves were in maximal diurnal position Amputation of the tips of axes led to local exudation of liquid, but was unattended by the occurrence of any petiolar movements 4.30 P M —The leaves were in full nocturnal position Amputation of the tips of axes was followed by extensively propagated movements of deepest petiolar depression along the course of the injured shoot

In comparing the results of experiments carried out respectively in the morning and evening it cannot, of course, be maintained that all the differences which are present—that all the phenomena of increased "irritability" in the evening—are to be credited to the coincident depression in assimilatory activity alone; for, as a rule, the conditions in the evening are much more favourable to rapid transpiratory loss than they are in the morning During periods of continuous settled weather diurnal atmospheric humidity attains its minimum in the afternoon and evening, whilst in the morning it is still relatively high This is shown by the figures in the following table of averages, derived from a series of weekly observations for the years 1892 93 with which my friend Mr C Little has kindly furnished me —

Average atmospheric humidity at various times of day. 100=*saturation.*

1892.

	6 A M	8 A M	10 A M	4 P M.	10 P M
January	90 2	85 7	62 5	40 5	78 25
February	84 5	71 4	48 6	35 0	74 8
March	88 0	75 6	48 75	31 0	71 75
April	87 8	77 75	63 0	54 0	81 0
May	89 0	79 2	70 6	59 2	85 2
June	92 0	82·25	73 25	73 75	90 0
July	96 0	90 25	86 75	83 0	92 5
August	94 8	89 0	80 4	78 4	91 4
September	95 75	85 5	77·25	77 75	92 5
October	95·2	82 6	72 6	65 6	91 4
November	87 7	77 75	59 5	47 0	92 0
December	86·25	79 5	53 25	35 75	88 25
Annual averages ...	90 6	81 3	66 3	56 9	85 75

1893.

	6 A M	8 A M	10 A M	4 P M	10 P M
January	93 0	90 0	63 0	40 6	83 4
February	94 75	87 5	71 75	63 0	91 0
March	94 25	88 25	60 0	54 5	83 25
April	91 25	80 75	64 75	54 0	85 25
May	89 2	81 0	69 20	59 8	81 40
June	92 75	86 25	84 50	82 75	89 25
July	92 8	88 0	84 40	82 40	89 0
August	94 0	87 5	81 0	77 0	90 5
September	95 25	90 25	85 25	82 75	82 75
October	92 8	84 0	78 25	73 25	94 0
November	85 5	76 75	62 0	57 5	92 0
December	94 25	82 25	64 25	50 25	91 25
Annual averages ..	92 4	85 2	72 8	64 7	88 2

The evening depression of atmospheric humidity and the consequent increased facility for transpiratory loss must, of course, tend to facilitate the occurrence and diffusion of rapid movements connected with fluctuations in turgescence, but at the same time it tends to give rise to a very considerable reduction in distal leverage, which must more or less equilibrate the increased instability connected with increased transpiratory loss, so that on the whole the evening rise in petiolar "irritability" may be fairly credited to decreased retentive power in the pulvinar tissues incident on diminished osmotic property in the cell-sap. That this is, at all events, the main determinant of the rise in "irritability" which normally presents itself in the evening is, moreover, demonstrated by the phenomena which present themselves during periods of prolonged and more or less continuous rainfall, when both soil and air are practically saturated and transpiratory loss is necessarily reduced to a minimum. Under such circumstances it will be found that, whilst amputation of the tips of terminal pinnules during the day, and whilst the leaves are in maximal diurnal position, is followed only by very limited and imperfect movements of pinnular elevation, purely confined to the injured pinna and unaccompanied by any movements of petiolar depression save in the case of leaves which are heavily loaded with adherent water, a similar injury in the evening and when the leaves have already completely assumed the nocturnal position is constantly followed by the deepest petiolar depression quite apart from the presence of any extrinsic distal loading. The effects of simple mechanical "stimulation" also vary very conspicuously in degree at different times of day. The leaves of seedling plants in the morning and early forenoon, so long as they are not exposed to the influence of direct sunshine and its attendant excess in transpiratory loss, are very highly elevated and exceedingly irresponsive to mechanical impulses, whilst in the evening, when the pinnules and pinnæ are in their maximal nocturnal position, the primary petioles remain very highly elevated, but very readily undergo the deepest depression on contact.

In the previous experiments we have been dealing with cases in which we have evidence of increase in "irritability" coincident with decreased assimilatory activity connected with the removal of solar stimulation; but parallel phenomena present themselves in cases in which protoplasmic activity is depressed, not by the absence of normal stimuli, but in consequence of exposure to the influence of anæsthetics. In order to the proper comprehension and interpretation of such phenomena it is necessary to have some acquaintance with the effects which follow exposure to simple desiccated atmospheres and simple exposure to anæsthetic vapours, as the evidences of increased "irritability" connected with the latter manifest themselves most clearly in cases of sudden exposure to a desiccated atmosphere containing vapour of chloroform. The data which follow are accordingly derived from three distinct sets of experiments. In the first of these plants were exposed to the atmosphere of a hermetically sealed chamber containing a vessel of pure sulphuric acid; in the second they were exposed to a humid atmosphere containing chloroform vapour; in the third they were exposed to the desiccated atmosphere of a chamber containing both chloroform and pure sulphuric acid.

Experiment IV.—A pot-plant, in a pot which had been waxed and luted as if for experiments on transpiratory loss, was enclosed in a hermetically sealed chamber containing a vessel of pure sulphuric acid and exposed to diffused sunlight. The leaves passed into the maximal diurnal position, but were extremely "irritable," movements attending the slightest mechanical disturbance, and the momentary application of flame to the tips of terminal pinnules being followed, not merely by complete movements throughout the injured leaf, but by propagation of movements to several other leaves. The soil in the pot was sufficiently moist, and the proportion of root-surfaces to foliar surfaces was sufficient, to permit of the maintenance of the maximal diurnal position in spite of very active transpiratory loss; but the equilibrium was a very unstable one, and consequently movements were very readily induced under the influence of any factors either favouring increased filtration in the tissues of the motor organs, or any sudden increase in transpiratory loss, or abnormal escape of liquid from the tissues incident on injury.

Experiment V.—A pot-plant was set within a common hermetically sealed chamber containing a vessel including a plug of cotton-wool soaked in chloroform. The leaves slowly and gradually assumed the nocturnal position more or less completely, and after some time death of the entire plant occurred. In this case the assumption of the nocturnal position was clearly simply owing to the action of the anæsthetic in depressing assimilatory activity; for the plant was throughout exposed to abundant diffused sunlight, and the atmosphere of the chamber must very soon have become more or less saturated owing to transpiration from the leaves and evaporation from the moist soil in the open pot.

EXPERIMENT VI —The basal and terminal portions of the solitary axis of a small pot plant were carefully protected and the central portion was enclosed in a space containing the vapour of chloroform A gradual assumption of the nocturnal position followed by death occurred in the leaves of the central exposed portion of the axis, which itself ultimately died and became brown, whilst the leaves on the basal and distal protected portions rapidly resumed the diurnal position, from which they had departed in connection with the initial disturbance to which they had necessarily been subjected, and retained it unaltered after the central portion of the axis and its leaves had been completely killed On the following day, and after the central part of the axis had been dead for many hours the leaves on the basal and distal portions were in normal diurnal position, and the application of heat to the base of the axis was followed, not merely by movements in the leaves situated to that side of the dead central area, but by *propagation of movements to those which were situated beyond it.*

EXPERIMENT VII —A plant in a common open pot was enclosed within a sealed chamber containing a vessel of strong sulphuric acid, so as to secure the occurrence of continuous, active transpiratory loss After the expiry of half an hour, and when the leaves were in maximal diurnal position, a plug of cotton wool saturated with chloroform was introduced into the chamber A complete assumption of the nocturnal position occurred within two hours, the movements leading to it being of an insensibly slow, progressive character

EXPERIMENT VIII —A plant in a carefully waxed and luted pot, so as to secure maximal transpiratory loss, and whilst the leaves were in full diurnal position, was suddenly introduced into a chamber containing vessels of both strong sulphuric acid and chloroform After a brief interval numerous pinnules in several leaves underwent sudden, rapid elevation The pot was now removed from the chamber, and, when all the pinnules were once more in maximal diurnal position, was again introduced into the chamber After a considerable interval had elapsed, numerous pinnules became abruptly elevated throughout almost all the pinnæ of all the leaves, but no depression of the primary petiole occurred in any case

EXPERIMENT IX —A plant in a luted pot, and with its leaves in maximal diurnal position, was suddenly introduced into a chamber like that employed in the previous experiment After an interval of about *half a minute, rapid spreading elevation of the pinnules set in* in many pinnæ The elevation was, however, incompletely carried out No depression whatever occurred in any of the primary petioles

EXPERIMENT X —A pot plant, luted in the usual fashion for experiments on transpiration, was introduced into a sealed chamber containing vessels of chloroform and of water No rapid action whatever occurred, but merely very slow, insensibly progressive elevation of the pinnules After it had remained within the chamber for a short time it was removed and, after the pinnules had completely recovered their normal diurnal position, introduced into a sealed chamber containing vessels of chloroform and of pure sulphuric acid Rapid movements of elevation presently occurred in a number of pinnules, and, after an interval, the primary petiole of the uppermost leaf, the pinnules of which were still in a condition of permanent elevation, underwent rapid depression

EXPERIMENT XI —A pot plant, luted as usual and with its leaves abundantly bedecked with adherent drops of rain, was introduced into a sealed chamber containing vessels of chloroform and of sulphuric acid After an interval of fifty seconds some pinnules in one leaf became relatively slowly and partially elevated, and after a further interval of two minutes all the pinnules of one pinna of another leaf acted in a similar fashion. Elsewhere only slow, insensibly progressive pinnular elevation occurred

The results of this series of experiments clearly demonstrate the following facts —

I —Exposure to the influence of anæsthetics under certain circumstances is attended by the occurrence of movements of precisely the same character as those which are ordinarily regarded as depending on stimulation and active contraction of the protoplasts of the motor organs

II —The rate at which movements occur under the influence of exposure to the vapour of chloroform varies with the degree to which facilities for the rapid transpiratory removal of water from the tissues are present

III.—Exposure to the influence of the vapour of chloroform under circumstances favouring rapid transpiratory removal of water from the tissues constantly occasions rapid movements in pinnules, but only exceptionally induces rapid movements of primary petioles.

IV.—Neither exposure to a desiccated atmosphere, unless the aridity be very extreme, nor exposure to a humid atmosphere containing the vapour of chloroform is capable of inducing rapid, sudden movements; but exposure to a desiccated atmosphere containing the vapour of chloroform is constantly attended by occurrence of such movements.

V.—The effects following exposure to the influence of the vapour of chloroform, even in cases where the treatment has been pushed so far as to cause actual death, are purely localised to those areas of a plant which are directly exposed to the vapour; and the death of comparatively large areas in an axis resulting from prolonged exposure neither affects the conduction of water by the water-conducting system, nor interferes with the propagation of the conditions which give rise to the occurrence of movements.

These facts are quite inexplicable on any theory which ascribes the occurrence of rapid movements of the leaves to stimulation and active contraction of the protoplasts of the motor organs. We have no ground for believing that exposure to anæsthetic vapours leads to stimulation of protoplasmic activity of any kind, but we have distinct evidence that it acts in precisely opposite fashion. Were the movements dependent on stimulation of contractile protoplasts in the motor organs by the anæsthetic vapour, they ought to retain the same character, no matter what the hygrometric properties of the atmosphere be; whereas as a fact sudden rapid movements never occur so long as the atmosphere is humid, and constantly manifest themselves when it is desiccated, although similar *atmospheric* aridity alone is incapable of inducing them, or indeed of inducing any movements whatever. Moreover, were the movements dependent on protoplasmic stimulation and active contraction, the fact that rapid pinnular movements are phenomena of normal occurrence on exposure to a desiccated atmosphere containing vapour of chloroform, whilst rapid petiolar movements are absolutely exceptional, would remain a hopeless mystery.

But on the theory that the movements are dependent on losses in turgescence *in the tissues of* the motor organs connected, not with any active protoplasmic contraction, but either with decrease in the osmotic capacity of the cell-sap, or with influences facilitating local filtration within the tissues of the motor organs, or disturbing pre-existent relations of equlibrium between general supply and loss of water, all the phenomena become readily explicable. Where plants or portions of plants are exposed to the influence of the vapour of chloroform in a saturated or practically saturated atmosphere (as in the case of experiments V, VI, and X) pinnular movements occur; but they are of the slow insensibly progressive character normally present in cases where diminutions in turgescence occur in connection with decrease or removal of normal stimulation. *They are of the same character* as those occurring periodically in connection with the diminution and cessation of solar stimulation at sundown. They are evidently dependent solely *on the gradual* loss of osmotic capacity in the tissues of the motor organs attending the depression of assimilatory activity caused by the action of the anæsthetic. Where (as in experiment VII) conditions favouring transpiratory loss are considerably greater, the rate of movement increases, because here the escape of liquid from the interior of the cells of the motor organs accompanying depression of protoplasmic functional activity is facilitated by continuous evaporative loss from the tissues generally. Where, finally (as in experiments VIII, IX and XI), depression in osmotic capacity is associated with exposure to a desiccated atmosphere, conditions providing for relatively rapid, considerable fluctuations in turgescence are manifestly present; and with this suddenly executed movements make their *appearance*. Such movements are not, however, evenly distributed throughout the different parts of the leaves. They occur constantly in the pinnules, quite exceptionally in the primary petioles, and never, in so far as my experience goes, in the pinnæ. Are we to suppose that the vapour of chloroform under certain circumstances constantly acts as a stimulant to the protoplasts of the tertiary pulvini, whilst *it* does so only occasionally to those of the primary pulvini and has no stimulant effect whatever on those of the secondary ones? It is surely

more reasonable to account for the phenomena as the result of a perfectly uniformly depressant factor affecting the assimilatory activity of the protoplasts of all the motor organs alike, but whose effects manifest themselves in unlike fashion in parts which differ from one another in structural peculiarities and in their relations to other parts of the leaf Loss in osmotic capacity, and excessive transpiratory loss, work hand in hand in making for the elevation of the pinnules, which is determined by the excessive structural strength of the inferior mass of parenchyma in the tertiary pulvinus, the same factors come into play locally to give rise to a tendency towards depression of the primary petiole, but here the weakening of the inferior mass of pulvinar parenchyma is discounted by the coincident diminution in the resistance which it has to overcome connected with the simultaneous decrease in distal leverage attending excessive transpiratory loss Finally, in the secondary pulvini there is an absence of any highly developed differences in the structural and functional properties in the masses of tissue which make respectively for divergence and convergence, and with this any liability to the occurrence of rapid movements necessarily diminishes Mere exposure to the influence of vapour of chloroform is incapable of inducing sudden movements, exposure to a desiccated atmosphere, unless the degree of aridity be very excessive, is equally inefficient but the loss of osmotic property connected with the depression of functional activity caused by the action of the vapour of chloroform facilitates the occurrence of losses of turgescence to such an extent as to ensure the occurrence of rapid movements wherever conditions favouring active transpiratory removal of water are present in high degree

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APPENDIX D.

ON CERTAIN COMMONLY ACCEPTED BUT ERRONEOUS STATEMENTS REGARDING PHENOMENA PRESENTED BY *MIMOSA PUDICA*

I.—That, in the initial nocturnal position of the leaves during the earlier portions of the night, the primary petioles are in a position of deep depression *

THE following notes give the results of observations in regard to this point, which were carried out at various times of year —

EXPERIMENT I —January 27th 6 P M Pinnæ and pinnules in maximal nocturnal position Primary petioles highly elevated, but becoming deeply depressed on contact impulses

EXPERIMENT II —January 28th, 6-20 P M
EXPERIMENT III —February 1st, 6 20 P M
EXPERIMENT IV —February 8th, 6 P M
EXPERIMENT V —February 11th, 6 P M
} Results precisely similar to those of the previous day

EXPERIMENT VI —May 30th, 7 P M. Pinnæ and pinnules in maximal nocturnal position Primary petioles horizontal or slightly elevated

EXPERIMENT VII —October 11th, 6 P M Pinnæ and pinnules almost in maximal nocturnal position Primary petioles horizontal or slightly elevated

October 11th, 8 30 P M Pinnæ and pinnules in maximal nocturnal position Primary petioles horizontal or slightly elevated.

October 12th, 12 15 A M Pinnæ and pinnules as before Marked increase in elevation of the primary petioles

The observations of the 27th and 28th January and of the 1st, 8th, and 11th February were conducted in regard to very young plants in which the numbers of pinnæ and of pinnules in the leaves were still small, the pinnæ, as a rule, being only two or three in number and bearing only a limited number of pinnules. This probably accounts for the fact that in all cases the primary petioles were highly elevated, as in such leaves, apparently in connection with deficiency of distal leverage, excessive elevation of the primary petiole is of constant occurrence The laminar portions

* Sachs Vorlesungen, Vorlesung XXXVII, s 789

of the leaves of seedling plants are for some time very feebly developed, there being only from one to two pinnæ present, and these bearing only a very few pairs of pinnules, so that distal leverage is probably much less influential in them than it is in fully developed leaves with their four pinnæ and multitudinous pinnules.

The phenomena which are presented by the leaves of *Mimosa pudica*, when grown under normal tropical conditions, and especially when grown in the open ground so as to permit of indefinite extension of root-surface, certainly render it very hard to imagine how a belief in the occurrence of deep depression of the primary petiole as a normal nyctitropic phenomenon should have arisen. Had it been present, it would have been quite anomalous and a striking example of an exception to the rule that the position of the various parts of nyctitropic leaves during the earlier part of the night is one which was either the permanent position in very young leaves or the diurnal position in somewhat older but still immature ones. But, as a matter of fact, deep petiolar depression does not occur. And the slightly ascending, horizontal, or slightly descending position which really does occur affords a striking example, not of deviation from, but of conformity to, that rule. The position, however, even in plants with unlimited extension of root-surface, is normally an extremely unstable one owing to the coincident depression of osmotic capacity within the pulvinar tissues at a time when they have still to contend with very considerable distal leverage; and hence very slight disturbances, which are quite incapable of inducing deep depression in unloaded leaves exposed to solar stimulation, readily suffice to give rise to it now. As has been pointed out in Appendix C, the disturbance in the liquid-equilibrium in an axis which attends the amputation of its distal extremity gives rise to much *more constant and extensively propagated movements of petiolar* depression when it occurs after the leaves have assumed the initial nocturnal position than when it comes into play whilst they are still subject to solar stimulation and in the maximal diurnal one. This, perhaps, affords an explanation of the origin of the belief; for it is conceivable that deep petiolar depression may spontaneously occur in the case of pot-plants with limited root-surfaces and exposed to abnormally dry nocturnal atmospheres, the limitation of supply of water and continued active transpiratory loss co-operating to play the part of slight mechanical disturbances or other extrinsic agencies disturbing the liquid-equilibrium of the tissues. Even if this be the case, however, it in no way affects the fact that, under normal circumstances, deep depression of the petiole is not a normal nyctitropic phenomenon.

*II.—That when the primary petiole is deeply depressed during the day in consequence of "stimulation," its leaf hangs loose and pendulous; whereas when in the same position during the early part of the night it is rigid.**

It is hardly necessary to discuss this question, seeing that, in plants grown under normal circumstances, the position of deep depression of the petiole, whether it arises diurnally or nocturnally, makes its appearance under precisely similar circumstances and is induced by the same factors. It may, however, be pointed out that it is not true in regard to plants grown under normal circumstances that the leaves hang loose and pendulous when petiolar depression has arisen diurnally in consequence of the action of any so-called "stimulant" agencies.

III.—That sudden exposure to absolute darkness, apart from any other disturbing conditions, is attended by the occurrence of sudden movements in the leaves.

The following notes show the nature of the results of experiments in which plants, whose leaves were in maximal diurnal position, were suddenly introduced into the absolute darkness of a photographic dark-room in which black velvet curtains covered even the small windows of coloured glass affording the only source of light under ordinary circumstances:—

EXPERIMENT VIII.—After an exposure of five minutes' duration no appreciable change in the position of the various parts of the leaves had occurred. After an exposure of fifteen minutes a certain

* Sachs Vorlesungen; Vorlesung, XXXVII, s. 789.

amount of pinnular elevation was recognisable After an exposure of thirty two minutes the pinnule occupied a position more or less intermediate between their normal maximal diurnal and nocturna positions No perceptible alteration in the positions of the primary petiole occurred throughout th entire course of the experiment

EXPERIMENT IX —No immediate effect followed transfer to the dark room After an exposur of thirty minutes the pinnules occupied a position almost intermediate between the maximal diurna and nocturnal positions at the close of an hour the pinnæ and pinnules were almost in maxima normal nocturnal pos t on, but the primary petioles remained elevated

Repeated experiments of a like nature unequivocally showed that mere deprivation of light however sudden and complete it be, is never an efficient factor in giving rise to the occurrence o sudden movements, and that it is in itself unattended by the occurrence of deep petiolar depressio even where it has acted during periods prolonged enough to secure maximal convergence of the p nn and elevation of the pinnules They further showed that elevation of the pinnules occurs somewha more rapidly in plants exposed to a dry atmosphere than in those exposed to a humid one, and, conversely that recovery of the diurnal position on renewed exposure to light occurs more rapidly in a humi than in a dry atmosphere

In the case of experiments of this nature we have to deal with movements connected with th incidence of external influences determining fluctuations in the functional activities of the tissues of th motor organs, but the fluctuations are of a negative not of a positive nature, they are dependent not o the incidence, but on the removal of stimulation, and the decrease in turgescence of the tissues of the moto organs which directly determines the displacements of the various parts of the leaves is caused not by active contraction of the protoplasts of the tissue elements, but by the elastic recoil of th cell walls, *which is no longer efficiently opposed owing to the decreased osmotic property of the cell sap* The movements are of a slow and insensibly progressive character, as is the case with all movements arising under similar circumstances In all cases in which the occurrence of movements tending towards th assumption of the nocturnal posit on in the leaves of *Mimosa pudica* can be unequivocally traced t alterations in protoplasmic functional activity acting alone, the displacement is invariably of a slov gradually progressive character, and in all cases it is connected not with st mulation, but with depressio of protoplasmic activity Sudden exposure to absolute darkness implies sudden deprivation of solar stimu lation of the protoplasts of the tissues, and with this a sudden depression of assimilatory activity, but th effects of this do not manifest themselves suddenly, because assimilatory activity is only indirectly relate to the maintenance of maximal turgescence through the intervention of the osmotic properties which i confers upon the cell sap owing to the products which it adds to it The deprivation of solar stimulatio places an arrest on the assimilatory addition of osmotic products to the cell sap, but the actual loss in turgescence ultimately ensuing on this will be regulated by the progress of expenditure of the osmoti products present at the time at which the arre t took place The deprivation of the conditions se urin maintenance of turgescence at a certain standard is sudden, but the fall in turgescence is gradua because it is connected with the gradual expenditure of a stock of pre existent unstable materials So in the case of plants which are exposed to the influence of the vap ur of chloroform in a humi atmosphere gradual progressive movements alone occur, because here again we have to deal only wit depression and ultimate abolition of assimilatory activity leading to loss of osmotic capacity of the cel sap, and through this to alterations in the turgescence of the tissue elements But, whilst depressio of functional activity is incapable when acting alone to give ri e to the occurrence of sudden move ments, it may serve to secure their occurrence when it co operates with other conditions favourin losses in turgescence, but equally incapable of inducing the occurrence of sudden movements when actin alone The sudden introduction of a pl nt into a desiccated atmosphere is, as a rule, followed merel by very slow progressive movements of the pinnules, or, in cases where the root supply of water i very abundant, may be unattended by any movements whatever but sudden introduction into a chambe containing both sulphuric acid and chloroform is normally followed by the occurrence of sudden rapidl executed movements, because here we have to deal not merely with conditions depressing functiona activity or giving rise to great increase in transpiratory loss but with conditions implying the coinci dent presence of both these factors of decrea e in turgescence Are we to suppose, as the ordinaril

accepted theory of the induction of suddenly executed movements would apparently demand, that the vapour of chloroform becomes a stimulant to functional activity in a dry atmosphere, whilst it acts as a depressant in a moist one? Surely it is more rational to conclude that in both cases it acts alike as a depressant of functional activity, but that the rate at which indices to its action manifest themselves in a reduction of turgescence varies with the extent to which facilities for the rapid removal of water from the tissues are present.

*IV.—That the nocturnal position of the various parts of the leaves is one which is connected with a degree of turgescence in the motor organs greater than that which is present in connection with the diurnal position.**

In order to demonstrate the groundlessness of this belief it is only necessary to call to mind the phenomena which can be directly observed in the guard-cells in connection with the assumption of the diurnal and nocturnal condition by the stigmatic orifices, together with the fact that the nocturnal position is assumed by the leaves of *Mimosa pudica* under the influence of anæsthetics or of conditions implying excess in transpiratory loss in relation to root-supply of water.

APPENDIX E.

THE INFLUENCE OF HYGROMETRIC CONDITIONS ON THE DEGREE OF "IRRITABILITY" OF *MIMOSA PUDICA*.

The effect of hygrometric conditions in influencing the degree of liability to the occurrence of rapid and extensively diffused movements in the leaves of *Mimosa pudica* is illustrated by the following experimental data. The experiments are arranged in two distinct groups, *A* and *B*; those included under *A* illustrating the character and extension of the movements following the incidence of so-called "stimulant" agencies under conditions of excessive atmospheric and telluric moisture; those under *B* illustrating the phenomena presenting themselves under the influence of similar agencies when humidity was normal or depressed.

GROUP A.—HUMIDITY EXCESSIVE.

a.—Results following amputation of tips of terminal pinnules of distal pinnæ, or amputation of tips of axes.

1.—Effects following the amputation of the tips of pinnules.

EXPERIMENT I.—June 23rd. *Temperature 77·5°F., atmospheric humidity 97 per cent. Rain had fallen steadily for some hours and was still falling heavily; everything drenched with moisture.*—Amputation of the tips of terminal pinnules was followed by a pause, during which drops of exudation appeared at the divided extremities of the mid-rib and the larger veins on the cut surface. Elevation of the injured pinnule, of its fellow, and of one or two adjacent pairs of pinnules followed slowly. Partial elevation subsequently occurred in one or two others, but pinnular movements never extended along the entire course of the injured pinnæ.

EXPERIMENT II.—July 19th. *Temperature 80°F., atmospheric humidity 97 per cent. Continuous rain had fallen during the previous night and continued to fall gently at the time of experiment. Everything was drenched with moisture. The leaves were in maximal diurnal position and, in many cases, were heavily loaded with adherent drops of rain.*—Amputation of the tips of terminal pinnules was followed by very slow and irregular action in a certain number of pinnules. Frequently only two or three distal pinnules

* Sachs Vorlesungen; Vorlesung, XXXII, s. 789.

became elevated, and elevation of the injured pinnule was often delayed until visible exudation had appeared on the cut surface In the case of heavily loaded leaves depression of the primary petiole usually occurred, the movement immediately succeeding elevation of the injured pinnule, or of it and its fellow

EXPERIMENT III —July 20th *Temperature 80 5°F, atmospheric humidity 95 per cent Heavy rain had fallen all night and rain was still falling at the period of experiment Everything was drenched with moisture* —Amputation of the tips of terminal pinnules of leaves which were not loaded with adherent drops of rain was followed only by imperfect elevation of a few distal pinnules in the injured pinnæ No action whatever occurred even in the injured pinnule until after a pause, during which drops of exudation appeared on the cut surface

EXPERIMENT IV —July 25th *Temperature 78°F, atmospheric humidity 94 per cent Very heavy rainfall had occurred shortly before and the sky was still covered with clouds Everything was drenched with moisture The leaves were in maximal diurnal position and many of them were heavily loaded with adherent drops of rain* —Amputation of the tips of terminal pinnules was followed merely by slow and imperfect action in a few of the distal pairs of pinnules in the injured pinnæ, save in the case of heavily loaded leaves, in which deep depression of the primary petiole occurred simultaneously with or immediately after elevation of the injured pinnule

EXPERIMENT V —August 7th *The day was one of drenching, tropical showers alternating with intervals of brilliant sunshine The leaves were in maximal diurnal position and in some instances heavily loaded with adherent drops of rain* —Amputation of the tips of terminal pinnules was followed merely by very slow and imperfect action in eight or nine neighbouring pairs, and, in the case of one heavily loaded leaf, by deep depression of the primary petiole ere any but the injured pinnule had become elevated Here all the conditions for excessive turgidity of the tissues were certainly present, for there had been abundant solar stimulation in coincidence with excessive root supply and minimal transpiratory loss, and yet "irritability" in place of being maximal as Haberlandt says it ought to be under such circumstances, was minimal

EXPERIMENT VI —September 13th *Almost uninterrupted rainfall had taken place during the three previous days and drenching showers had fallen earlier in the morning The sky was bright, but the sun was veiled by cloud Everything was drenched with moisture The leaves were in maximal diurnal position and in many cases loaded with adherent drops of rain* —Amputation of the tips of terminal pinnules was followed by a pause, during which no movements occurred, but drops of exudation appeared at the divided extremities of the mid rib and larger veins of the injured pinnule Slow elevation of the injured pinnule then took place This was succeeded by a pause, after which the uninjured terminal pinnule acted Another pause ensued, followed by slow movements of elevation in a certain number of pinnules in the outer half or third of the injured pinna In the case of heavily-loaded leaves depression of the primary petiole often occurred as the first sequence to elevation of the injured pinnule and its fellow, and in one case as the very first phenomenon of movement subsequent to exudation on the cut surface of the injured pinnule

EXPERIMENT VII —October 7th *Very heavy rainfall had occurred in the course of the previous night and during the earlier part of the day The leaves were in maximal diurnal position* —Amputation of the tips of terminal pinnules was followed by very slow elevation of the pinnules of the injured pinna, the movements being in many cases confined to the terminal third or half of its course The primary petiole in some cases became depressed immediately after elevation of the injured pinnule and its fellow

2 *Effects following the amputation of the tips of axes.*

EXPERIMENT VIII —June 24th, 8 A M *Heavy showers of rain had fallen during the night and both soil and air were very humid* —Amputation of the tips of axes was attended by no results, save the local exudation of a large drop of fluid on the divided surface

EXPERIMENT IX —July 15th, 8 A M *Air very moist and ground saturated owing to heavy rain on the previous day* —Amputation of the tips of axes was followed merely by the exudation of a large drop of fluid on the cut surface

Experiment X.—August 20th, 1 a.m. *Heavy showers had fallen in the course of the morning and both soil and air were very humid.*—Amputation of tips of axes was merely followed by local exudation of liquid on the cut surface.

b.—Results following mechanical disturbance or separation from the axis.

Experiment XI.—A pot-plant was introduced into a sealed moist chamber and exposed to diffused sunlight. Extreme elevation and expansion of the leaves occurred, and when the whole apparatus was violently shaken, so as to agitate the leaves strongly, the only movements which occurred were confined to a certain number of pinnules which were actually in contact with the walls of the chamber.

Experiment XII.—June 10th. *Rain was falling heavily and everything was drenched with moisture.*—A pot-plant was conveyed over a mile of rough road without the leaves showing any appreciable departure from their normal diurnal condition, in spite of the continuous, agitation to which they were exposed during the transit.

Experiment XIII.—June 24th. Conditions and results as in the previous experiment.

Experiment XIV.—August 3rd. *Then and during several previous days atmospheric humidity was excessive and rainfall abundant.*—A vigorous shoot was detached from a plant and conveyed over a mile of rough road intervening between the garden in which the plant grew and the laboratory. It bore nine leaves, the two terminal ones being still very young. In spite of the continuous agitation to which it was exposed *en route*, it reached the laboratory with the primary petioles of all the leaves save one either horizontal or only very slightly depressed, and all the pinnules, save one or two isolated ones, in almost maximal diurnal position. Even half an hour later the pinnules were only partially elevated; but, on exposure to a gentle current of warm dry air, they rapidly assumed the fully-developed nocturnal position.

Experiment XV.—September 24th. *Almost continuous drenching rain had fallen during the previous forty-eight hours. The sky was covered with cloud. Everything was drenched with moisture and the leaves were in maximal diurnal position.*—Separation of shoots from the plants to which they belonged was attended by no movements whatever in the leaves unless they were subjected to violent agitation.

c.—Results following the application of flame to the tips of terminal pinnules of distal pinnæ.

Experiment XVI.—A pot-plant was enclosed within a sealed moist chamber. After it had remained within it for some time the cover of the chamber was several times momentarily partially displaced and an open flame applied to the tips of the terminal pinnules of one of the distal pinnæ of several leaves. The application was followed by the occurrence of slow movements, in some cases extending over the entire leaf, in others confined to the injured pinnæ. In no case was there any propagation of movement to any leaf but the injured one. When similar treatment was applied to the leaves of plants growing in the open air, complete movements in all cases occurred throughout the whole of the injured leaf, and action was invariably propagated to at least one other leaf, although atmospheric humidity was at the time by no means low.

Experiment XVII.—A plant was treated as in the previous experiment. When flame was applied to one or two of the terminal pinnules of one of the lower leaves, slow and partial elevation occurred in all the pinnules of all the pinnæ, and was followed by depression of the primary petiole; but there was no propagation of movement to any other leaves. When similar treatment was applied to the leaf of a plant in a luted pot within a sealed sulphuric acid chamber, complete and rapid action occurred throughout the whole of the injured leaf and was propagated to all the other leaves on the plant.

Experiment XVIII.—A pot-plant was placed in a sealed moist chamber. The leaves became extremely elevated and expanded. After an interval of two hours and a half, the cover was partially removed and flame was applied to the tips of the terminal pinnules of a distal pinna of one of the leaves. Slow and partial action occurred throughout the injured leaf, but there was no propagation of movement to any other leaves. When similar treatment was applied to a plant which had been for

some hours in a sulphuric acid chamber, rapid and complete action took place throughout the injured leaf and was propagated to all the other leaves on the single axis of which the plant was composed

EXPERIMENT XIX.—June 12th *Soil very moist, atmospheric humidity high*—The application of flame to the terminal pinnules of distal pinnæ of leaves of plants growing in the open ground was followed by very slow and imperfect elevation of the pinnules of all the pinnæ, and by slow and incomplete depression of the primary petiole There was never any propagation of movement to any other leaf

EXPERIMENT XX—June 9th *Rain was falling heavily and the soil was saturated with moisture*—The application of flame to terminal pinnules of distal pinnæ was followed by slow and imperfect elevation of all the pinnules of all the pinnæ of the injured leaf, and, in the case of one leaf which was heavily loaded with adherent drops of rain, by depression of the primary petiole No propagation to any other leaf occurred

EXPERIMENT XXI—June 15th. *The sky was completely covered with cloud, and heavy falls of rain were occurring at frequent intervals The soil was very moist*—The application of flame to the tips of terminal pinnules was followed by very slow, incomplete elevation of the pinnules of all the pinnæ and very slow, incomplete depression of the primary petiole of the injured leaf No propagation of movement to any other leaf occurred in any case

EXPERIMENT XXII—June 10th, 8 A M *Atmospheric temperature 80 5°F Humidity 92 per cent The morning was cool and still Heavy rainfall had occurred just before the period of experiment. There was brilliant sunshine, but the plants were not directly exposed to it*—The application of flame to the tips of terminal pinnules of distal pinnæ was followed by slow and almost complete elevation of the pinnules of the injured pinna, and by slow, imperfect action in the opposite distal pinna and in the proximal pinna on the same side as the injured one No action whatever occurred in the pinnules of the remaining pinna or in the primary petiole, and there was no propagation of movement to any other leaf

EXPERIMENT XXIII—June 21st, 8 A M *Atmospheric temperature 81 5°F. Humidity 91 per cent The sky was completely covered with cloud, but no rain had fallen during the night, and the leaves were consequently dry*—The application of flame to the tips of terminal pinnules of distal pinnæ was followed by complete action throughout the injured leaf, save in one case in which no action occurred in the proximal pinna of the opposite side of the leaf, and another in which the primary petiole did not undergo any depression No propagation of movement to any other leaves occurred

EXPERIMENT XXIV—June 23rd 8 A M *Atmospheric temperature 77 5°F. Humidity 97 per cent Rain had fallen continuously for some hours previous, and was still falling heavily Everything was drenched with moisture*—The application of flame to the tips of terminal pinnules to the extent of actually charring them was followed by slow action of the pinnules, never extending over more than three pinnæ, and, where the leaves were not heavily loaded with adherent drops of rain, usually unattended by any depression of the primary petiole In no case was there any propagation of movement to any other leaf

EXPERIMENT XXV—June 26th 8 A M. *Atmospheric temperature, 81 5°F Humidity 90 per cent The leaves were dry, but the soil was drenched with moisture The morning was bright, but there was an absence of direct sunshine*—The application of flame to the tips of terminal pinnules of distal pinnæ was followed by slow but almost complete elevation of all the pinnules of the injured pinna, depression of the primary petiole, partial action in the pinnules of the proximal pinna of the injured side and in those of the opposite distal pinna In one or two instances incomplete elevation also occurred in the pinnules of the remaining pinna In no instance was there any propagation of movement to any other leaf

EXPERIMENT XXVI.—June 29th 8 A M *Atmospheric temperature 79 5°F Humidity 94 per cent Rain was falling heavily*—The application of flame to the tips of terminal pinnules was followed only by very slow elevation of the pinnules of the injured pinna, and by incomplete elevation in those of the remaining ones Depression of the primary petiole did not occur, and there was no propagation of movement to any other leaf

d—Effects of the application of heat to a point in the course of a mature axis.

EXPERIMENT XXVII—July 20th, 8 A M *Atmospheric temperature 80 5°. Humidity 95 per cent Heavy rain had fallen all night, and rain was still falling Everything was drenched with moisture.*—The

thorough application of the points of heated forceps to points in the course of mature axes was followed in every case by an entire absence of any movements in any leaves either in the centripetal or the centrifugal direction. This experiment clearly proves that no mere fluctuations in pressure in the liquid contained in Haberlandt's "Reizleitende system" are efficient to occasion any propagation of movements. The local application of heat must here, as usual, have given rise to an elevation of pressure within the liquid contained in the system of sieve-tubes, and as usual this elevation must have been propagated in both directions, and yet no movements whatever took place either centripetally or centrifugally. The absence of the occurrence of any centrifugally propagated movements under such circumstances is readily explicable if we regard the centrifugal propagation which is ordinarily present as the result of obstruction to the ascent of water along the water-conducting system incident on the great gaseous expansion caused by the local application of heat. Under the circumstances prevailing at the time of the experiment not only must the entire water-conducting system have contained an excess of water, but transpiratory loss of water must have been practically absent. But this being so, there is no reason why a temporary obstruction or arrest in the passage of water along the water-conducting system should have given rise to the occurrence of any centrifugal propagation of movement; for, with minimal transpiratory loss and the presence of large quantities of reserve-water within the water-conducting system, there was no immediate demand for continuous root-supply in order fully to meet the demands of the motor organs, and the temporary obstructive effect of the gaseous expansion might well have entirely disappeared ere such a demand arose.

EXPERIMENT XXVIII.—July 24th, 8 A.M. *Atmospheric temperature 78·5°F. Humidity 94 per cent. The morning was cloudy. Very heavy rainfall had occurred shortly before the period of experiment and everything was drenched with moisture.*—Searing points in the course of mature axes was followed only by slow imperfect action in the first leaf beyond the injured point.

GROUP B.—HUMIDITY MODERATE OR LOW.

a.—Results following amputation of terminal pinnules of distal pinnæ, or amputation of tips of axes.

1. *Effects following the amputation of tips of pinnules.*

EXPERIMENT XXIX.—Complete elevation of all the pinnules of all the pinnæ and deep depression of the primary petiole of the injured leaf.

EXPERIMENT XXX.—Complete action throughout the whole of the injured leaf.

EXPERIMENT XXXI.—Complete action throughout the whole of the injured leaf and depression of the primary petiole of the one next above it on the axis.

EXPERIMENT XXXII.—Complete action throughout the whole of the injured leaf.

EXPERIMENT XXXIII.—Complete action throughout the whole of the injured leaf.

EXPERIMENT XXXIV.—Complete action throughout the whole of the injured leaf; almost complete action throughout the whole of the leaf next above it on the axis.

EXPERIMENT XXXV.—Complete action in the injured leaf and in the one next above it on the axis.

EXPERIMENT XXXVI.—Complete action in the injured leaf, followed by complete action in the one next below and the one next above it on the axis.

EXPERIMENT XXXVII.—Complete action in the injured leaf, followed by complete action in the one next below and the one next above it on the axis.

EXPERIMENT XXXVIII.—Complete action throughout the whole of the injured leaf.

EXPERIMENT XXXIX.—Complete action throughout the whole of the injured leaf.

EXPERIMENT XL.—Complete action throughout the whole of the injured leaf; complete action in the first leaf above it on the axis; depression of the primary petiole and partial elevation of the pinnules of the third leaf above the injured one.

2. *Effects following amputation of tips of axis.*

EXPERIMENT XLI—Action in the first four leaves beneath the tip, and action in five other leaves situated at some distance lower in the course of the same shoot

EXPERIMENT XLII—Centripetal propagation of movement to all the leaves on the same shoot

EXPERIMENT XLIII—Centripetal propagation of movement to all the leaves on the same shoot

EXPERIMENT XLIV—Centripetal propagation of movements to the nine leaves situated immediately beneath the tip along the course of the same shoot

EXPERIMENT XLV—Centripetal propagation of movement to all the leaves on the same shoot.

b.—Results following the application of flame to the tips of terminal pinnules of distal pinnæ.

1. *Plants rooted in the open ground*

EXPERIMENT XLVI—Complete action throughout the whole of the injured leaf and the one next above it on the axis

EXPERIMENT XLVII—Complete action throughout the whole of the injured leaf and the one next above it on the axis

EXPERIMENT XLVIII—Complete action throughout the injured leaf and depression of the primary petiole of the one next below it on the axis

EXPERIMENT XLIX—Complete action throughout the injured leaf, complete action in one leaf below and in two above it on the same axis

EXPERIMENT L—Complete action in the injured leaf and in the two next above it on the axis

EXPERIMENT LI—Complete action throughout the injured leaf, incomplete action in two above and one below it on the same axis

2 *Pot plants*

In the case of pot-plants the effects following the application of flame to the tips of pinnules are much more extensively propagated, owing, no doubt, to their more limited root supply

EXPERIMENT LII—Complete action in the injured leaf, complete action in all the leaves above it and in one below it on the same axis

EXPERIMENT LIII—Complete action in the injured leaf, followed by complete action in all the other leaves over the entire plant

EXPERIMENT LIV—Complete action in the injured leaf, followed by complete action throughout all the leaves on the same axis

EXPERIMENT LV—Complete action in the injured leaf, followed by complete action in all the leaves on the same shoot save the lowest one

EXPERIMENT LVI—Complete action in the injured leaf and in the three leaves next above it on the axis

EXPERIMENT LVII—Complete action in the injured leaf and in all the others on the same axis

The following experiment illustrates the influence which differences in degree of soil moisture alone are capable of exerting on the nature of the phenomena attending the application of flame to the tips of terminal pinnules of distal pinnæ

EXPERIMENT LVIII—June 22nd *Atmospheric temperature* 84 5°F *Humidity* 77 *per cent*—Two pot plants, *A* and *B*, were standing side by side in the open air and were under precisely the same circumstances, save that the earth in the pot in which *A* was contained was dry, whilst that in the pot containing *B* was thoroughly moist in consequence of the recent addition of water

When flame was applied to the terminal pinnules of leaves of *A* complete action throughout the injured leaf, followed by the occurrence of movements in varying numbers of leaves situated along the course of the same shoot, occurred in every instance, whereas, when similar treatment was applied to leaves of *B*, it was followed merely by slow, imperfect elevation of all the

pinnules, succeeded in one instance by deep and in another by slight depression of the primary petiole of the injured leaf.

In this experiment we have evidence of the extent to which excessive root-supply may serve to discount the result nominally attending the presence of active transpiratory loss connected with moderate atmospheric humidity.

c.—Results following the application of heat to points in the course of mature axes.

Experiment LIX.—*Heat applied by focussing the rays of the sun upon a point in an axis 4 inches from the leaf next above it, and about 0·75 of an inch from the one next beneath it.*—Centrifugally propagated action occurred in all the eleven leaves situated on the distal side of the point of application. No action whatever occurred in any leaves on the basal side.

Experiment LX.—Centrifugally propagated action in all the leaves situated to the distal side of the point of application.

Experiment LXI.—Centrifugally propagated action in all the leaves situated beyond the point of application.

If we insist in regarding the movements which the leaves of *Mimosa pudica* exhibit under the influence of textural injuries or mechanical disturbance as necessarily dependent on stimulation and active contraction of the protoplasts of the motor organs, the results of this entire series of experiments must force us to the conclusion that the degree of irritability in the tissues is almost entirely regulated by the nature of the hygrometric conditions to which the plants are exposed, and runs parallel with the extent to which defective supply or excessive loss of water is present. It is, of course, possible to imagine that such a relation between protoplasmic irritability and hygrometric conditions might exist, but there is certainly nothing to explain why it should do so. But if we regard the movements as having no direct relation to functional activity, but as directly dependent on purely physical processes of redistribution of liquid throughout the tissues, it at once becomes evident that the presence of any external conditions favouring the occurrence of rapid disturbances in liquid equilibrium must necessarily also favour the occurrence of rapid movements. The series of coincidences is of such a nature that, whilst the ordinarily accepted theory is quite incapable of accounting for it, the physical theory can readily do so; and this being so, there can be no question that the latter has here, as in many other cases, the better claim to acceptance.

APPENDIX F.

ON THE EFFECTS WHICH FOLLOW THE LOCAL APPLICATION OF HEAT TO AREAS IN THE COURSE OF AXES OF *MIMOSA PUDICA*.

As has been pointed out in the body of this paper, the effects following the local application of heat to points in the course of axes of *Mimosa pudica* are different in the case of young, soft, green shoots from those which present themselves in mature, woody ones.* In both cases extensive centrifugal propagation of movement is constant; but in the former case centripetal propagation frequently occurs to a certain extent, whilst in the latter it is entirely absent, save in cases wherever the point of application is in the immediate neighbourhood of the first leaf below it, and then is confined to the latter. The following data are derived from a series of experiments on mature shoots in which heating was in some cases effected by means of the application of an open flame, in others by the employment of heated forceps, and in still others by focussing the sun's rays by means of a lens:—

a.—Effects following application of an open flame.

Experiment I.—*Flame applied midway between two leaves.*—Action in all the leaves beyond the point of application; no action whatever beneath it.

Experiment II.—*Flame applied as in the preceding case.*—Action as above.

Experiment III.—*Flame applied near the inferior leaf and at a considerable distance from the superior one.*—Action in all the leaves beyond the point of application, no action in any beneath it.

Experiment IV.—*Flame applied immediately above the inferior leaf and far from the superior one.*—Action in all the leaves beyond the point of application, and in the leaf immediately beneath it.

b.—Effects following the searing of a point in the course of an axis with strongly heated forceps.

Experiment V.—*Forceps applied to the axis close beyond an inferior leaf and far from the next superior one.*—Progressive centrifugal action of all the leaves along the course of the axis beyond the point of application, no action beneath the point of application.

Experiments VI, VII, VIII, IX, X.—Procedure and results identical with those of experiment V.

Experiment XI.—*Forceps applied immediately above the inferior leaf.*—Action in the first leaf beneath the point of application and in all those above it.

In a series of thirty similar experiments in which complete movements occurred in all the leaves on the axis beyond the point of application, movements occurred in the first leaf beneath it in only five instances, and in all of these the point of application was very close to the origin of the primary petiole from the axis.

c.—Effects following focussing the rays of the sun on a given point in the course of an axis.

Experiment XII.—*Focal point close to the origin of the leaf beneath and about two inches from the one next above it.*—Complete, spreading, centrifugal action in all the leaves above the point of application, no action whatever in any leaf beneath it.

Experiment XIII.—*Focal point close to the origin of the leaf beneath and about three inches from the one next above it.*—Complete action in all the leaves beyond the site of application, no action whatever in any leaf beneath it.

Experiment XIV.—*Focal point close to the origin of the leaf beneath it and about an inch and a half from the one next above it.*—Complete action in all the distally situated leaves, action in the leaf immediately beneath the site of application.

Experiment XV.—*Focal point about midway between the leaves beneath and above it.*—Action in all the nine leaves situated distally, no action whatever in any leaf beneath the point of application.

Experiment XVI.—*Focal point close to the origin of the leaf beneath it and about thirteen inches from the first one above it.*—Action in all four leaves situated distally, action in the leaf immediately beneath the point of application.

In a series of nineteen experiments of this nature, in which movements occurred either in all the distally situated leaves or in a considerable number of them, action only occurred beneath the point of application in five instances, and in all of these the point of application was very close to the origin of the petiole of the leaf next beneath it and movements were confined to the latter only.

As has already been pointed out in Appendix E, the results following the local application of heat to points in the course of an axis vary according to the conditions of atmospheric and telluric humidity prevailing at the time of experiment. When, as in the case of the experiments detailed above, humidity is moderate or low, the application is followed by very extensive centrifugal propagation of movements, extending frequently along the whole of the distal portion of the axis, but where this is no longer the case, propagation diminishes in extent and completeness, and where humidity attains maximal proportions, it may be attended by an entire absence of any appreciable movements whatever.

Experiment XVII.—The points of a pair of strongly-heated forceps were applied to an axis just after a heavy fall of rain. Spreading centrifugal action occurred in all the distally situated leaves, but the action was incomplete, for, whilst the primary petioles became deeply depressed, the pinnæ and pinnules showed only very slight displacements.

Experiment XVIII.—July 20th, 8 a.m. *Atmospheric temperature 80.5°F. Humidity 95 per cent. Heavy rain had fallen during the course of the previous night, rain was still falling gently at the time of experiment, and everything was drenched with moisture.*—The tips of a strongly heated pair of forceps were

applied to several axes, but in no instance was the application followed by the occurrence of any appreciable movements, either centrifugally or centripetally.

EXPERIMENT XIX.—July 25th, 8 A.M. *Atmospheric temperature 78·5°F. Humidity 94 per cent. The morning was cloudy; very heavy rain had fallen shortly before and everything was very wet.*—Searing of axes was followed only by very slow, imperfect action confined to the first leaf beyond the point of application.

Now were the effects which, under average conditions of humidity, follow the application of heat to axes dependent on the propagation of stimulant fluctuations in pressure conducted along any closed system of tubes containing liquid such as Haberlandt's "Reizleitende system," it is clear that, in place of diminishing and ultimately disappearing with increased humidity, they ought to increase as it increases. They ought to increase with any conditions favouring increased turgidity throughout the system, whereas in fact they follow a precisely opposite course. But such decrease and abolition of movement is precisely what ought to occur if the phenomenon of spreading centrifugal movement which occurs under ordinary circumstances be the outcome of an obstructive gaseous interference with the current of water ascending from the roots. Under ordinary conditions of atmospheric and telluric humidity there is no accumulation of surplus water within the water-conducting system, and the stream traversing the latter only suffices to maintain full turgescence of the tissues in spite of continuous transpiratory loss. Under such circumstances any obstruction to the continuity of the stream must at once tend to disturb the pre-existent equilibrium between supply and loss of water in all distally situated parts; and as the diurnal position of the leaves is dependent on maximal turgescence in the tissues of the motor organs, any disturbance of this nature must inevitably tend to cause a departure from it. But where conditions of atmospheric and telluric humidity are maximal, root-supply becomes excessive and transpiratory loss is reduced to a minimum, and with this a surplus stock of water must tend to accumulate within the water-conducting system. The latter no longer represents a simple system of channels traversed by a stream of water which escapes at the distal extremity in the same bulk as it enters at the proximal one, but a reservoir containing a large store of water from which only a very small quantity is constantly being withdrawn. The bulk of water contained within the water-conducting system is greatly in excess of that which is continuously withdrawn from it to maintain full turgescence under the conditions of minimal transpiratory loss, and consequently the occurrence of a temporary obstruction of root-supply is of no consequence in respect to the maintenance of turgescence. The diurnal position of the leaves is determined by the fact that certain masses of tissue in the motor organs are endowed with excessive assimilatory and osmotic properties under the influence of solar stimulation. But the application of heat to a point in an axis does not affect the assimilatory and osmotic properties of the motor organs of the leaves in any way, and consequently, so long as the water-conducting system contains a supply of water from which they can satisfy their osmotic capacities, there is no reason why any fluctuations in their turgescence should attend the application. Now a store of surplus water has accumulated within the water-conducting system under the influence of the previous and existent conditions of humidity, so that a temporary obstruction to the access of any additional supply is of no importance whatever in regard to the maintenance of turgescence, and consequently no movements attend its establishment. The absence of movements in this case is precisely parallel to the absence of movements attending the separation of leaves or shoots from a plant under conditions of excessive humidity. In both cases alike there is an arrest of root-supply of water; but, in the case of detachment, not only is the arrest an absolute and permanent one, but it is accompanied by a certain amount of active loss of liquid from the cut end of the petiole or shoot; whereas on the application of heat to the tissues of a mature axis mere temporary obstruction to root-supply is present. In both cases alike the maintenance of the turgescence of the motor organs is for the time being fully provided for by the local store of water within the water-conducting system; and consequently any brief, temporary arrest of root-supply is incapable of inducing the occurrence of any movements, and any permanent one can give rise to movements only after the gradual expenditure of the surplus water stored up within the water-conducting system. In neither case does any immediate effect follow the arrest of root-supply; and where the arrest is only temporary and renewed supply sets in ere expenditure of the store-water has occurred, no movements at all will occur. Where,

on the other hand, the arrest is a permanent one, movements of a slow, insensibly progressive character will ultimately set in in consequence of the gradual fall in turgescence attending the expenditure of the surplus water

APPENDIX G.

EXPERIMENTS DEMONSTRATING THE PROPAGATION OF THE CONDITIONS GIVING RISE TO MOVEMENTS THROUGH AREAS OF DEAD TISSUE DEVOID OF ANY LIVING PROTOPLASM OR SYSTEM OF TURGID SIEVE TUBES

EXPERIMENT I —An axis of *Mimosa pudica* was thoroughly seared at two distinct levels by means of the application of the points of a strongly heated pair of forceps The higher seared area measured 0 39" and the lower 0 3" in length, and subsequent microscopic examination showed that in both the tissues had been entirely killed throughout the entire thickness of the axis One leaf arose from the portion of the axis between the two seared areas, and several others were situated below the lower and above the upper one After the leaves had completely recovered the normal diurnal position, an open flame was applied to the tips of the terminal pinnules of one of the leaves beneath the lower seared area of the axis, and universal propagation of movements took place, all the leaves on the axis, those beneath the lower seared area, the one between the two seared areas, and those beyond the upper one alike showing rapid petiolar depression and pinnular elevation

EXPERIMENT II —An area 0 5" in length in the axis of a small pot plant was thoroughly seared with heated forceps On the following day the seared area was perfectly dead, dry and brown, but the leaves, both below and above it, were in full, normal, diurnal position When flame was applied to the tips of the terminal pinnules of a distal pinna on one of the leaves beneath the seared area complete action occurred in it, and propagation of movements presently followed throughout the entire course of the axis

EXPERIMENT III —An axis was thoroughly seared at two points in its course On the following day all the leaves were in normal, diurnal position The application of flame to the tips of the terminal pinnules of a distal pinna of one of the leaves beneath the lower seared area was followed by movements extending over all the leaves on the axis including one arising between the two seared areas The length of each of the seared areas was about 0 45" and microscopical examination showed that the tissues had been thoroughly killed throughout the entire thickness of the axis

EXPERIMENT IV —A pot plant, consisting of a single axis bearing six leaves, was thoroughly seared and killed at two points, one situated between the second and third leaves from the base of the axis and the other between the third and fourth leaves After all the leaves had completely recovered the normal diurnal position, the tips of a pair of heated forceps were applied to the base of the axis and rapid centrifugal propagation of movements presently occurred in all six leaves

EXPERIMENT V —A plant was treated in the same way as that of the preceding experiment After complete recovery of the normal diurnal position the application of the point of heated forceps to a point near the base of the axis was followed by complete propagation of movements to all the leaves along its course, beneath, between, and above the seared areas

Such experiments conclusively prove that the propagation of movements along the course of axes is neither dependent on any continuous tracts of living protoplasm, nor on the existence of any continuous system of turgid tubes along the course of which sudden fluctuations in pressure may be transmitted The thorough searing of the tissues of the axis implies not merely local death, but local absence of turgidity in the tissues The seared areas, in place of any longer being sites of active turgescence, are sites which afford abnormal facilities for the escape of liquid from the tissues, as is clearly indicated by the fact that, unless under conditions of excessive atmospheric humidity, the leaves which are situated distally soon begin to indicate the presence of insufficient water supply by their incapacity to assume the maximal diurnal position The thorough searing of the tissues of the axis just as effectually interrupts the continuity of the turgid system of sieve tubes as any local excision of the bast does, and

yet it in no way affects the propagation of movements attending the establishment of sudden abnormal drain on, or obstruction to, root-supply of water to the tissues. Haberlandt assumes that, in cases in which propagation of movement continues in spite of an interruption in the continuity of the bast, the conveyance of the impulses across the hiatus is effected by the wood; so that, in cases in which propagation traverses several seared areas in an axis, he must assume that the impulses follow a complicated zigzag course alternately in the bast tubes and the wood. Even apart from the phenomenon of the purely centrifugal propagation of impulses in cases where heat is applied to points in the course of mature axes, the fact that propagation occurs readily, in spite of the presence of repeated interruptions in the continuity of the system of turgid sieve-tubes, shows conclusively that the latter is in no sense a specific apparatus for the conduction of the conditions which give rise to the occurrence of movements.

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PLATES

PLATE I

Fig 1	*Selaginella serpens*		Portion of inferior surface and margin of leaflet, showing strong rigid marginal frame	× 310
Fig 2	*Ditto*	*ditto*	Under surface of leaflet, central portion	× 160
Fig 3	*Ditto*	*ditto*	Upper surface of leaflet, stained with vesuvin, showing porous character of cells	× 310
Fig 4	*Ditto*	*ditto*	Superior surface of leaflet, morning	× 310
Fig 5	*Ditto*	*ditto*	Ditto ditto, after sundown	× 310
Fig 6	*Ditto*	*ditto*	Ditto ditto, ditto	× 160
Fig 7	*Ditto*	*ditto*	Ditto ditto, midnight	× 160
Fig 8	*Ditto*	*ditto*	Ditto ditto, after exposure in a chamber containing sulphuric acid and chloroform	× 310
Fig 9	*Ditto*	*ditto*	Superior surface of leaflet, morning	× 660
Fig 10	*Ditto*	*ditto*	Ditto ditto, after sundown	× 660
Fig 11	*Mimosa pudica*		Position of a young, immobile leaf at an early stage of development, natural size	
Fig 12	*Ditto*	*ditto*	Position of a somewhat more mature, immobile leaf, natural size	
Fig 13	*Pithecolobium saman*		Extremity of a growing axis, showing positions of young immobile leaves	
Fig 14	*Ditto*	*ditto*	Primary pulvini of leaves of various ages on an axis, natural size	
Fig 15	*Ditto*	*ditto*	Vertical sections of primary pulvini of various ages, showing gradual development of superior parenchyma, natural size	
Fig 16	*Ditto*	*ditto*	Tertiary pulvinus of a young, immobile pinnule, longitudinal, vertical section	× 50
Fig 17	*Ditto*	*ditto*	Tertiary pulvinus of a mature, freely mobile pinnule, longitudinal, vertical section	× 50
Fig 18	*Mimosa pudica*		Position of a young leaf just before the onset of nyctitropic movements	
Fig 19	*Cassia alata*		Secondary pulvinus, vertical section, showing the disposition of the opposing masses of pulvinar parenchyma.	

PLATE II

Fig 1	*Cassia alata*	diurnal position of pinnæ from a photograph	
Fig 2	*Ditto*,	nocturnal position of pinnæ, from a photograph	
Fig 3	*Ditto*,	vertical, transverse section of basal portion of secondary pulvinus, natural colours.	
Fig 4	*Ditto*,	diagram of the base of the outer half of a pinna attached to its rachis viewed from the under surface, showing laminar expansion of pulvinus	
Fig 5	*Ditto*,	pulvinus and base of the lamina of a pinna viewed from the under surface with the keel of the mid rib and pulvinus removed, showing the expansion of pulvinar tissue over the base of the outer half of the lamina . . .	× 10

Fig. 6. *Bauhinia corymbosa*; secondary pulvinus; transverse vertical section of laminar expansion in the nocturnal position . . . . × 50

Fig. 7. *Ditto* *ditto*; secondary pulvinus; tissue of under surface of petiolar portion . × 400

Fig. 8. *Ditto* *ditto*; ditto ditto; tissue of upper surface of petiolar portion . × 400

PLATE III.

Fig. 1. *Cassia sumatrana*; extremity of growing axis; showing positions of the various parts of the leaves ere nyctitropic movements begin to occur.

Fig. 2. *Ditto* *ditto*; secondary pulvinus and base of lamina of a pinna viewed from the under surface; showing the spiral disposition of the opposed masses of pulvinar parenchyma . . . . × 10

Fig. 3. *Ditto* *ditto*; secondary pulvinus and base of lamina of a pinna viewed from the under surface; showing spiral arrangement of the opposed masses of pulvinar parenchyma . . . . × 10

Fig. 4. *Ditto* *ditto*; portion of a leaf; showing diurnal position of mature but still nyctitropic pinnæ, and the purely local effects of exposure to the vapour of chloroform; twenty-four hours after the lower portion of the rachis and the lower pair of pinnæ had been exposed to the action of the vapour of chloroform and when the lower pair of pinnæ were dead and flaccid, and the upper pair quite turgid and in normal diurnal position.

Fig. 5. *Leucaena glauca*; transverse vertical section of primary pulvinus showing the very excentric position of the fibro-vascular axis . . . . × 25

Fig. 6. *Ditto* *ditto*; ditto ditto ditto ditto . . × 10

Fig. 7. *Ditto* *ditto*; extremity of growing axis; showing the positions of the various parts of leaves ere nyctitropic movements are present.

Fig. 8. *Ditto* *ditto*; transverse vertical section of secondary pulvinus; showing circular outline and relative strength of the fibro-vascular axis . . . . × 10

Fig. 9. *Ditto* *ditto*; transverse horizontal section of secondary pulvini of a distal pair of pinnæ.

Fig. 10. *Ditto* *ditto*; pinnules beginning to assume the nocturnal position; showing pulvinar expansion over base of under surface of outer half of lamina . . . . × 10

PLATE IV.

Fig. 1. *Pithecolobium saman*; primary pulvinus, vertical transverse section; from a very young leaf; showing excess of *inferior* parenchyma . . . . × 10

Fig. 2. *Ditto* *ditto*; primary pulvinus, vertical transverse section; from a mature leaf; showing excess of *superior* parenchyma . . . . × 10

Fig. 3. *Ditto* *ditto*; secondary pulvinus, vertical, longitudinal section; showing excess in thickness and in chlorophyll content of the inferior parenchyma . . . . × 20

Fig. 4. *Ditto* *ditto*; secondary pulvinus, vertical transverse section; showing great vertical compression of fibro-vascular axis . . . . × 25

Fig 5 *Pithecolobium saman*, secondary pulvini and rachis, vertical transverse section, showing the relation of the inner side of the inferior masses of parenchyma to the bevelled surfaces of the rachis . . . . . × 10
Fig 6 *Ditto* *ditto*, secondary pulvinus; *a*, tissue of inferior, *b*, of superior parenchyma . . . . × 520
Fig 7 *Ditto* *ditto*, tertiary pulvinus, vertical transverse section of distal portion, showing excess of chlorophyll in superior parenchyma of a thick, opaque section . . . . × 25
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Fig 9 *Ditto* *ditto*, tertiary pulvinus, *a*, tissue of superior, *b*, of inferior parenchyma . . . . × 520

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ERRATUM

Page 74, line 2 *For* "whereas, &c," *read* where, as in the secondary pulvini of *Pithecolobium saman*, it takes the form of a flattened band, the superior and inferior masses exceed it in vertical diameter, and the lateral ones fall short of it in horizontal diameter,

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A NEW AND PARASITIC SPECIES

OF

CHOANEPHORA

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By

D D CUNNINGHAM, M B, F R S, C I E

Brigade-Surgeon Lieutenant Colonel Bengal Army

WITH TWO PLATES

CALCUTTA

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1895

A NEW AND PARASITIC SPECIES

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In the early part of September 1894 my attention was directed, by a gentleman, resident in Calcutta, to the presence of a destructive blight affecting plants of *Ipomœa rubro cœrulea*, Hook in his garden Entire leaves or large portions of leaves and axes suddenly acquired a pale colour and presently wilted and died off, so that, during the period when the blight was at its maximum, the growth of the plants was practically brought to a standstill, the newly developed leaves and shoots not doing more than replacing the older ones which were constantly being killed off The extension of the blight was greatly influenced by the character of the atmospheric conditions prevalent at the time During periods of continuous cloud and rain with maximal atmospheric humidity it spread with great rapidity, whilst at times when sunshine prevailed and the air was relatively dry its progress was very much slower It continued to show itself more or less conspicuously according to the state of the weather, during the whole course of September and October, and then disappeared with the onset of cool and dry weather in November I was at first inclined to suppose that is was connected with the presence of one of the various species of Sclerotinia, or other closely allied fungi, which occur so abundantly as blights during the latter part of the rainy season, but even very cursory examination was sufficient to show that this was not the case

On examining the affected parts before they had become dry and brown, the surfaces could be seen to be clothed with numerous colourless, erect filaments with brown dilated extremities (Plate VIII, Fig 1), and these under the microscope revealed themselves as fructifying filaments emerging from the stomatic orifices and bearing numerous brown conidia on capitula closely resembling those of *Choanephora Cunninghamiana*, Currey (Plate VIII, Fig 2, Plate IX, Fig 25) Both filaments and capitula were, however, smaller than normal in that species, and the masses of conidia were of a pure vandyke brown colour and had not the purplish tint characteristic of those proper to it (Plate VIII, Figs 2, 22, Plate IX, Fig 25)

At this stage no mycelium whatever is present on the surface of the affected tissues, but at a later period and when numerous conidia have already fallen, the germinal tubes, which rapidly emerge from these under favourable circumstances, may be present in considerable numbers The characters of the mycelium which is present within the tissues of the host plant are essentially of a mucorine type The most satisfactory demon stration of this is obtained in vertical longitudinal sections through the thickness of axes, as the course of individual filaments can be more readily traced in these than in

sections of the laminar tissues. In such sections the whole depth of the green hypodermal tissue is seen to be permeated by enormous mycelial tubes (Plate VIII, Figs. 12—17). The larger of these run more or less parallel with the length of the axis and are crowded with vacuolate, coarsely granular, colourless or pale ochreous protoplasm exhibiting very active streaming movements. The largest tubes give off numerous somewhat finer branches which are provided with flattened haustorial processes closely applied to the outer surfaces of neighbouring cells (Plate VIII, Figs. 12*b*, 14, 16, 17). Here and there branches pass off obliquely towards the epidermis, and, when they reach substomatic spaces, dilate and completely fill these. One or sometimes two processes are given off from this swelling and force their way out through the stomatic orifice to form secondary dilatations beyond it, and from these the fertile filaments are in their turn given off (Plate VIII, Figs. 12*a*, 13). The filaments become somewhat dilated terminally so as to form a capitulum, and from this a number of conidiiferous capitella corresponding to those of *Choanephora Cunninghamiana* are given off. In detail, however, the characters of the capitella are very distinct in the two species. When mature the capitella of the species here dealt with are abruptly truncate and resemble the conidiiferous cells of *Botrytis cinerea* Pers., rather than the rounded capitella of *Choanephora Cunninghamiana*. Moreover, when the conidia become detached the capitella never form the beautiful funnels from which the genus derives its name, which is no doubt owing to the original difference in their form and to the absence of any appreciable differences in the thickness of the walls over their lateral and terminal surfaces. The number of capitella present in different instances varies considerably, but in many cases may amount to ten or more. The truncate extremity becomes covered with short sterigmata each of which gives origin to a conidium. The conidia when mature are very deciduous and fall off much more readily than those of *Choanephora Cunninghamiana* do, this being partially, no doubt, owing to the absence of funnels. In artificial cultures in nutritive infusions the conidial fructification comparatively rarely makes its appearance, and when it does occur is feebly developed. The capitula are small and the capitella few in number, or they may both be completely suppressed and the sterigmata arise directly from the stem in more or less peronosporoid fashion (Plate IX, Fig. 10).

The conidia when mature have average dimensions of 0·015×0·008 m.m. They are fusiform in outline and are provided with a finely longitudinally striate epispore, differing thus both in form and structure from the conidia of *Choanephora Cunninghamiana* (Plate IX, Figs. 1, 17, 18). This conidial fructification is the only one which I have ever met with on the plant as a parasite on *Ipomæa rubro-cærulea*, but probably zygospores may be produced within the tissues when external conditions cease to favour the production of conidia. Under favourable conditions, however, during its parasitic existence the mycelium produces conidial fructification alone and in enormous profusion; that is to say, it only produces that form of fructification which is associated with excessive nutrition and vegetative growth. Both in regard to this species and to *Choanephora Cunninghamiana* the result of artificial cultures appears conclusively to show that nutritional conditions are the main factors determining the particular form which the fructification shall assume in individual instances. Where very abundant nutritive supply is present purely vegetative growth occurs; short of this conidial fructification makes its appearance; with greater diminution of supply the sporangial and zygosporic fructifications tend to appear; and, finally, in the presence of minimal nutrition chlamydospores alone are produced.

The species is certainly capable of parasitic existence on other hosts than *Ipomœa rubro-cærulea* The conidia or sporangial spores when sown on the petals of the common *Zinnia elegans* and kept in a moist atmosphere germinate freely, giving origin to germinal tubes which penetrate the tissues and very rapidly cause their death, producing a crop of fructification which, although not so vigorous as that occurring on *Ipomœa rubro cærulea*, is still of conidial type In this it differs from *Choanephora Cunninghamiana* the conidia or spores of which when sown on Zinnia flowers fail to give rise to any blighting of the latter As I have more than once observed Zinnias affected by what on casual inspection I took to be *Choanephora Cunninghamiana*, there can be little question that these flowers occasionally play the part of natural hosts to the other species

The diffusion of the blight in *Ipomœa rubro cærulea* seems to be mainly determined by direct contact with previously affected tissues, blighted portions of axes serving as sources of infection of adjoining healthy ones, and the adhesion of blighted and wilted leaves to healthy ones or to healthy axes being followed by the appearance of the disease in the latter

In artificial cultivations whether in infusions of *Ipomœa rubro cærulea* or of the flowers of *Hibiscus rosa sinensis*, the conidial fructification is ordinarily entirely suppressed, and, when it does make its appearance in connection with greatly concentrated media, it is only feebly developed Very few heads of normal type are developed, and these at utmost bear a very limited number of capitella In most instances the conidia arise directly from the primary capitulum, or even this is suppressed, and they arise simply from the undilated tip of the stem, or at short intervals from one another in its neighbourhood, so that the fructification comes to present an almost peronosporic character (Plate IX, Fig 10) In certain cases only a single terminal conidium may be present (Plate IX, Fig 10)

When cultivated in infusions of the leaves of *Ipomœa rubro cærulea* or of the flowers of *Hibiscus rosa sinensis* of moderate strength, or on boiled petals of the latter plant, sporangic fructification is developed in great abundance, either alone or associated with varying numbers of zygospores, and it is only in extremely concentrated infusions, specially of *Hibiscus*, that conidial fructification also begins to make its appearance in association with the sporangic one The abundance of sporangia produced in cultivations in media of average quality is excessive Under normal circumstances they are produced in far greater numbers and attain a much greater size than those of *Choanephora Cunninghamiana* ever are or do (Plate VIII, Figs 3, 20, Plate IX, Fig 15) At an early stage of development they are of an amber colour owing to the tint of the sporangic membrane, but on ripening they become first brown and ultimately almost black owing to the dense accumulation of the brown spores which are formed within them (Plate VIII, Figs 3, 20) The stem is ordinarily abruptly flexed immediately beneath the origin of the sporangium, so that the latter looks more or less downwards On maturing, the sporangia dehisce in valvular fashion allowing the spores to escape, whilst the two halves of the membrane remain attached to the tip of the stem on either side of the large columella (Plate VIII, Fig 19) The sporangic membrane is ordinarily finely tuberculate

The spores are very peculiar Like the conidia they are fusiform in outline and provided with a finely striate brown epispore (Plate IX, Fig 2) They have average dimensions of 0 0168×0 0089 m m, and are therefore relatively somewhat narrower than the conidia, and the brown tint of the epispore is as a rule somewhat deeper than

it is in the latter. They are at once definitely distinguishable from the conidia, and from the sporangic spores of the *Choanephora Cunninghamiana* (Plate IX, Figs. 13, 14, 20) owing to the fact that one or ordinarily both of the extremities is provided with a bundle of fine, long, radiant, colourless processes, which in some cases originate from a colourless protrusion and in others appear to emerge directly from a point at which the epispore is absent (Plate VIII, Fig. 19, Plate IX, Figs. 2, 4, 5). They strongly resemble the rudimentary mycelial processes of certain of the Rhizidieæ and seem to have a mycelial function as is indicated by the facts that the spores appear invariably to undergo a very considerable increase in size without corresponding vacuolation, like that occurring both in the case of the conidia and in that of the sporangic spores of *Choanephora Cunninghamiana*, previous to the emergence of germinal tubes, and also that, in cases where they are cultivated under conditions of defective nutrition, a chlamydospore is not unfrequently developed as a direct extension of the intrasporic protoplasm (Plate IX, Fig. 5). When the latter is the case the parallelism of the spores to Rhizidieal organisms becomes very striking indeed, because, as will presently be shown, the chlamydospores on germinating in most cases give direct origin to sporangiferous filaments.

The epispore of the spores and that of the conidia, in cases in which the latter undergo any considerable increase in bulk ere germinating, is ruptured ere the emergence of a germinal tube, a phenomenon which does not attend the germination of either the conidia or spores of *Choanephora Cunninghamiana* (Plate IX, Figs. 16, 20). The rupture does not, however, follow the same course in the two cases. In that of the spores it takes the form of irregular fissuring, whilst in the case of the conidia the epispore is broken up into a number of distinct fragments (Plate IX, Figs. 3, 4). The occurrence of rupture of the epispore of the sporangic spores clearly shows that the occurrence of such a phenomenon in the case of conidia is no just ground for regarding the latter as parallels of unisporic sporangia; for, if the conidia are to be regarded as such on this ground, then in a case like the present the sporangic spores must be regarded in the same light, and this leaves the presence of the mother-sporangium unaccounted for. Even where conidiiferous filaments produce a single conidium only and the sporangia become unisporic, as is not unfrequently the case under the influence of defective nutrition, the difference between the two forms of fructification remains as sharply defined as ever (Plate IX, Figs. 10, 11).

On germinating the conidia give origin to one, or some times two, germinal tubes, which emerge apparently indifferently from any point of the surface. The spores, on the other hand, have never more than one tube, and this invariably originates laterally so as to leave the sites of origin of the radiant processes intact (Plate IX, Figs. 3, 4). When the medium furnishes sufficient nutritive supply, the germinal tubes of both sporangial spores and conidia alike rapidly lengthen, ramify, and give origin to a characteristic, aseptate mucorine mycelium. In cultivations in artificial media the mycelial filaments, although of considerable magnitude, and as a rule larger than those of *Choanephora Cunninghamiana* (Plate VIII, Fig. 18; Plate IX, Fig. 14), never attain the colossal proportions which many of them do when the plant occurs parasitically. The mycelium in artificial cultivations presently gives origin to an abundant crop of sporangiferous filaments, which appear first at the margins of the medium and afterwards, as the nutritive properties of the latter diminish, over its entire surface. In cases where the medium is highly concentrated a certain number of conidiiferous filaments are associated with

the sporangiferous ones, and in any average cultivation zygospores are liable to make their appearance in varying numbers There is nothing to indicate what is the essential determinant of the appearance of zygosporic fructification, for, in two cultivations conducted side by side in portions of one and the same specimen of a medium, zygospores may be entirely absent in one and almost entirely replace sporangia in the other When the medium is a very dilute one chlamydospores alone are produced (Plate VIII, Fig 21) The phenomena attending the germination of the chlamydospores differs in different instances In a certain number of cases they give origin to a mycelium like that originating from the spores and conidia, but in many instances no mycelium is formed and the germinal tube elongates directly into a sporangiferous filament (Plate IX, Figs 7 9) When the nutritive medium is not excessively poor, two or more chlamydospores may be formed in the course of individual mycelial filaments but, when the nutritive properties of the medium fall very low, each conidium or spore only gives origin to a single chlamydospore, and this in many cases is directly continuous with the parent body and forms a simple extension of the latter (Plate IX, Figs 5, 6)

The zygospores vary considerably in structural details even within one and the same culture In certain cases they are quite typically zygosporic, the two conjugating tubes which contribute to their formation being of equal value, alike in size and general appearance (Plate VIII, Figs 4, 5, 8), in others one of the conjugating elements is much larger than the other, the difference between them in certain cases becoming so excessive that in this respect the process comes to be rather of an oosporic than a zygosporic type (Plate VIII, Figs 6, 7, 9, 10), and in a few cases the spore appears to be of a truly azygosporic character and the product of a single mycelial process only (Plate VIII, Fig 11). In some instances the conjugating processes take origin from the same mycelial filament, in others from distinct ones, and whilst in some cases they are unaccompanied by any other peculiar processes, in others they are associated with varying numbers of short, often twisted processes (Plate VIII, Figs 5, 8), although these never are present in such numbers as to give rise to the formation of the complicated sclerotioid masses of tissue which are occasionally associated with the zygospores of *Choanephora Cunninghamiana* Another point of difference in the zygospores in the present as compared with the latter species is that the oosporic separation of the contents from the wall of the spore and their subsequent investment with a special membrane which is so frequent in *Choanephora Cunninghamiana* (Plate IX, Figs 21, 22) never appears to occur here

The colour of the contents of the conjugating processes varies from different shades of yellow to strong reddish, and not unfrequently, at a time when the contents of one process have already been completely accumulated terminally and separated by the formation of a partition, those of the other are present throughout its entire course and continuous with those of the parent mycelial filament (Plate VIII, Fig 7) The mature zygospores are of a deep brown or almost black colour and have average diameters of 0 0o7 m m They rarely contain any massive accumulation of oil in the form of a large globule, but, where such a body is present, it can be readily determined that the epispore, like that of the sporangial spores and conidia, is finely striate (Plate VIII, Fig 9)

The germination of the zygospores has not yet been observed, but, judging from the fact that the chlamydospores give direct origin to sporangic fructification whilst those of *Choanephora Cunninghamiana* produce a conidial one, it appears probable that they are the source of sporangia also

A special interest appears to attach to this species of Choanephora both because of its capacity for parasitic existence and because it contributes additional evidence that the genus to which it belongs is of a singulary generalised type showing special points of affinity to many other phycomycete and higher fungi.

Parasitism has, of course, long been recognised as occurring among zygomycete fungi in the genera Piptocephalis, Syncephalis and Chætocladium, but this would appear to be the first instance in which the occurrence of a zygomycete as a true parasite in a phanerogamic host has been recorded. It is somewhat difficult to determine whether the parasitism or the saprophytism should be regarded as "facultative." If we are to accept De Bary's view that the production of zygospores in one medium rather than another is the true criterion,* then the parasitism is "facultative," as zygospores certainly appear to be more readily produced in artificial media than in the tissues of the host plant. But it appears to be somewhat questionable whether this be a true criterion. Oospores and zygospores when produced by parasitic oomycete and zygomycete organisms are in many cases not produced until after the death of the host has been induced by the parasitism, which would appear to indicate that their production does not correspond with the presence of maximal nutritional facilities, but is rather indicative of a fall in these and in the activity of vegetative growth. Similarly, in the case of the purely saprophytic *Choanephora Cunninghamiana* zygospores are never produced until comparatively late in the duration of any culture and at a period when the nutritive properties of the medium have been in great part expended in providing for abundant mycelium and conidiiferous fructification. In so far as the Choanephoras are concerned, the true criterion of the presence of conditions favouring excessive nutritional activity and vigorous growth is the extent to which conidial fructification is produced. *Choanephora Cunninghamiana* in its normal site on the flowers of *Hibiscus rosa-sinensis* primarily produces nothing but excessive mycelial growth and conidiiferous fructification. It is only when the tissues of the flower have been greatly decomposed that zygospores make their appearance, and they also frequently occur abundantly in association with an impoverished conidial fructification in artificial cultivations in infusions of Hibiscus petals. When mycelial growth is very active and vigorous the conidiiferous fructification reaches its maximal development, and it is only when the conditions providing for maximal mycelial growth and fully developed conidiiferous fructification are absent that zygosporic fructification begins to appear. Turning to the second species of Choanephora, no one who has ever seen the enormous development which the mycelial system attains within the tissues of *Ipomœa rubro-cœrulea* as compared with that which it presents in infusions of the host-plant or of Hibiscus petals can entertain any doubt that the nutritional facilities provided by the artificial media are vastly inferior to those provided by the living tissues of the host-plant. But zygospores appear rarely or never to occur in the tissues of the host-plant when conditions are most favourable to mycelial extension and enormous production of conidiiferous fructification, whilst they occur in extreme abundance in many artificial cultivations, and in these are associated, not with the conidiiferous, but with the sporangic form of fructification, which in the case of *Choanephora Cunninghamiana* can be unequivocally demonstrated to be one which is associated, not with an excess but a defect of nutritional activity, being in fact the form of fructification which only appears with defective supply of nutritive materials and goes on showing itself until the defect

* Vergleichende Morphologie und Biologie der Pilze, Leipzig, 1884, s. 414.

becomes so great that chlamydospores alone are produced If, then, we take general nutritional activity rather than the production of sexual fructification as the true criterion, the Choanephora described in the present case ought to be regarded as a parasite endowed with "facultative" saprophytism, whilst if Dr Bary's standard be retained it must be regarded as a saprophyte endowed with "facultative" parasitism The phenomena appear to indicate that we have to deal with a transitionary stage between the pure saprophytism of the other species of Choanephora and pure parasitism, but one in which adaptation to parasitic existence has advanced so far that nutritional facilities are present in greater degree in the latter than when the plant occurs as a *saprophyte*

In this adaptation to parasitism on phanerogams the plant shows closer affinities to certain of the Oomycetes, such as Peronospora, than it does to any Zygomycete fungi In the one species of Choanephora we have to deal with a purely saprophytic organism retaining characters of more primitive type than those which are present where any special adaptation to parasitic existence has arisen, whilst in the other parasitism makes its appearance, not yet of such highly specialised type as to imply adaptation to one particular host, but yet so far evolved that growth attains its maximum in association with it In this respect the genus presents very generalised characters and forms a *connecting link between the parasitic and saprophytic Phycomycetes But it does* more than this, as it presents a curiously large series of affinities to distinct groups, both of the higher and lower fungi generally In *Ch anepho a Cunninghamiana* the normal type of fructification is certainly conidial, for conidial fructification occurs alone under conditions of high nutrition, and is the form which is directly derived from the chlamydospores, whilst sporangic fructification only occurs in association with very defective nutrition and is of a more or less abortive type But in the other species conidial fructification only occurs under conditions of excessive nutrition, and then does not attain such a high degree of evolution as it does in its ally, whilst the sporangic fructification *is developed under most circumstances, attains a high degree of evolution, and is that* which originates direct from the chlamydospores The former species has thus a special relation to the conidiferous series of higher fungi which culminates in the Basidiomycetes, and the latter to the sporangiferous series culminating in the Ascomycetes Special affinities to various groups of Phycomycetes are also indicated by the phanerogamic parasitism, the occasional Peronosporoid fructification, and the Rhizidiæoid character of the sporangial spores of the species here specially dealt with, and by the markedly oomycete characters which the sexual fructification of both species in many cases manifests The genus in fact in a sense appears to form a sort of centre from which various groups of both the *higher* and lower fungi radiate, and seems, therefore, to be *worthy of very special* attention In so far as its sexual fructification is concerned it is less specialised than the Oomycetes, and in respect to its conidiferous and sporangial fructifications less specialised than the two great groups of higher fungi have become, and it, therefore, seems to have in a sense retained ancestral characters in remarkably high degree

Choanephora Simsoni, Cunningham, n sp Conidia and spores fusiform, with a brown longitudinally striate epispore, spores provided with radiant terminal processes

Parasitic on *Ipomœa rubro cœrulea* Hook, and *Zinnia elegans*, saprophytic in various vegetable infusions, &c

Calcutta

DESCRIPTION OF PLATES.

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Fig 1 × 310



Fig 0



Fig 4 × 310

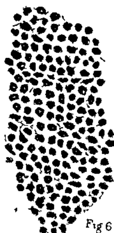


Fig 6



